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HERBERTIA

Journal of The International Bulb Society • Volume 57



2002-2003

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HERBERTIA

Journal of the International Bulb Society

VOLUME 57
2002–2003



International Bulb Society

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EDITOR'S NOTES

Would Hamilton P. Traub be shocked to find his offspring still alive and kicking after 57 years? I sometimes find myself pondering this question as I labor on HERBERTIA or engage with other IBS board members over some (occasionally unpleasant) bit of business. I don't have a facile answer to that question, however. Nonetheless, the International Bulb Society continues to chug along, despite officer turnover, personal politics, and ever present poverty. Why do we do this? While some might accuse us of a certain masochism, I would say we do this for one reason and one reason only. We think that IBS matters. We believe that the community of bulb enthusiasts wants something more than just a chat forum. And we believe that our publications provide a source of high quality information about geophytic plants unmatched by any other serial publication in the world. So, do I think that Dr. Traub would be shocked? Perhaps not. But I bet he would be at least pleasantly surprised.

Part of the struggle that IBS has maintaining its survival is the relatively low number of members that we have. Our publications are expensive to produce, and we generally come close to zeroing out the treasury every year now that we publish BULBS twice annually in addition to the yearly HERBERTIA. I would like to ask each IBS member a personal favor. If each and every one of you found one new member to join our society this year, we could double our membership in a heartbeat. Think what a boon that would be to our group – new faces, new voices, new bulb collections, and (of course) much-needed revenue that would allow our society activities to proceed more smoothly and regularly. That is the challenge I place before each of you for 2004. Bring one new member into IBS this year.

IBS and the bulb community at large lost a great friend this year, with the passing of Michael Vassar, after a long battle with cancer. Michael provided leadership on the IBS board or directors and edited HERBERTIA for several years. He will be sorely missed, and is this year's Traub Award winner.

Congratulations to our Herbert Medalist for 2002, Dr. Marcel Le Nard, one of the world's authorities on bulbous plant physiology. His volume with previous Herbert Medal winner, Dr. August de Hertogh, "The Physiology of Flower Bulbs," is a classic of horticultural science.

Astute readers will note a change to the year of volume starting in this issue of HERBERTIA. Henceforth, we will be using a two-year citation. The

reasons are mostly pragmatic; we have been dropping further behind in our schedule, and using this two-year system will give us a bit of "wiggle" room. Members paid up through 2002 will receive this volume. Volume 58 will be dated 2003–2004, and will be mailed to all members who have paid their dues in 2003, and so on. The first year in the volume will always be the indicator of which issue of HERBERTIA you should receive for dues paid in that annual period.

Please note that the final deadline for submissions for volume 58 (2003–2004) of HERBERTIA is June 1, 2004.

—Alan W. Meerow, Editor

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As a member of the **INTERNATIONAL BULB SOCIETY** you will receive the following yearly benefits:

The journal of the Society: **HERBERTIA**. The most comprehensive journal on bulbous plants in the world.

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Participation in the BX program. Periodic internet offerings of rare bulbs and bulb seed.

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Participation in occasional rare bulb sales. This will permit members to obtain rare and desirable species not available anywhere else.

Participation in our new **MEMBERS ONLY** section on the web site, where special offers and opportunities will be made only to members of the Society.

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THE HERBERT MEDAL



The Herbert Medal is the highest honor that the International Bulb Society can bestow upon a person for meritorious achievement in advancing the knowledge of bulbous plants. The medal is named for William Herbert (1778-1847), son of Henry Herbert, Earl of Carnarvon. William Herbert had a predilection for amaryllids and achieved success in their hybridization. He published his research findings in several monumental works. His contributions as a pioneer geneticist and plant breeder, and his arrangement of the Amaryllidaceae, helped set the stage upon which other workers, both amateur and professional, have been able to advance.

The award includes honorary life membership in the Society.

The Herbert Medal may be awarded annually or on special occasions by the Board of Directors of the Society. Medalists need not be members of the Society to be considered for the Herbert Medal.

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2002 HERBERT MEDALIST MARCEL LE NARD



I was born in 1940 in the village of Saint Eloy in Brittany, France. During my childhood, I had the opportunity to become familiar with plants on the small farm of my parents. I found some of them to be very intriguing as I watched them grow, flower, disappear, and grow again in the following year. This was especially true for the potato, a crop with which I would later become very familiar. I wondered how non-planted tubers were able to produce daughter tubers! At that time, producing food was the primary

objective. During that period, few ornamental plants were grown in gardens. However, I remember that we had some gladioli whose red dark flowers were very impressive. They looked like velvet. As a matter of interest, I must indicate that I had to learn the names of these plants, first in Breton, my maternal language, and later in French and Latin.

In 1959, I entered the Ecole Nationale d'Agriculture in Grignon, which is located close to Versailles and received my higher education. During those 3 years, I had the opportunity to become familiar with two topics: plant physiology and plant genetics. Ultimately, I selected plant genetics as my primary research interest. In 1962, INRA (Institut National de la Recherche Agronomique) provided me with the opportunity of joining the Plant Breeding Research Station in Versailles. For one year, I was involved in a sugar beet breeding program. During this period, I also completed my education in genetics at the University in Paris.

From early 1964 until April 1965, during my peace time service, I had the opportunity to go to Madagascar. There, I participated in a project involving the development and diversification of food supplies in villages in the Northwest of the country. One of the major projects was the development of gardens in the villages and the introduction of a wide range of vegetables. That was a very interesting experience.

In May 1965, I was asked by INRA to initiate a breeding program on flower bulbs. It was located in Ploudaniel, in Brittany, which is close to Brest. Up to that time, this research unit was involved only in potato breeding. I

started the research on flower bulbs in collaboration with my colleague Joseph Cohat. We decided to focus our programs on the tulip and gladiolus, the two major bulbous crops in France. We were very enthusiastic, but neither he nor I had any experience with ornamentals. This could be considered a handicap, but we rapidly discovered that it was an advantage since we had no prejudices about the crops. During the first two years we worked jointly. Then, we decided to specialize. Joseph took the leadership for the research on gladiolus and I devoted my efforts to tulips and Dutch iris.

When evaluating the needs for the tulip breeding program, it was rapidly concluded that there were two major problems: (1) the long juvenile period of the seedlings (5 to 6 years) and the consequent very low natural propagation rate that would make genetic studies very difficult, and (2) an efficient screening of the genetic material could be carried out only if we had a extensive knowledge of the influence of the environmental factors on the growth and the development of the tulip. The available literature, mainly from The Netherlands, indicated that temperature was the major environmental factor affecting tulip growth and that proper control of the bulb storage temperatures is necessary to influence flowering and bulb production. The literature also indicated that the major focus of the research had been devoted to flowering with the objective being the development of temperature treatments to obtain flowering in the winter, starting before Christmas. This research produced numerous "recipes" for forcers, however, very little was known about the physiological mechanisms underlying these results. I also noticed that the factors governing bulbing were not understood. Thus, research was initiated to determine the factors that affect the induction of bulbing. Subsequently, we were able to demonstrate that low temperatures were necessary to induce bulbing in tulips. We also determined that the effect of low temperatures appeared to be quantitative, i.e., that the induction of bulbing becomes stronger when the low temperature treatment is extended. In addition, it also appeared that under some conditions the induction of bulbing could be nullified by a subsequent high temperature treatment. Later, we showed that these results could also be obtained with Dutch iris. These results were initially published in a French scientific journal from 1968 to 1973.

In the early 1970's, I had the opportunity to meet Dr. E.J. Fortanier of the Agricultural University in Wageningen, The Netherlands and Prof. August De Hertogh of Michigan State University and later, North Carolina State University. With them, I had many very stimulating discussions that

convinced me to continue my research in this direction. Unfortunately, Dr. Fortanier died very early in his career, but the support persisted.

The initial studies also provided information on the type of experimental designs required for understanding the physiology of tulip and Dutch Iris. It appeared that only the use of very high (30–35°C) and very low (2–3°C) temperatures could separate these “inductive” processes from floral bud differentiation and growth processes whose manifestation is optimal at 15–20°C. Placing bulbs or plants under “abnormal” temperature conditions provided a very useful technique for understanding their behaviour under normal conditions. It was during this period that I concluded that having no experience with flower bulbs was very positive for conducting my research on flower bulbs!

Continued research on bulbing demonstrated that in the buds of a bulb, bulbing and organogenesis are exclusively different processes, i.e., meristematic activity ceases when bulb growth (scale primordia filling) begins. Active meristematic activity (bud differentiation) resumes only when bulb enlargement ceases. Thus, it was possible to distinguish between the two primary phases in the tulip cycle. First, there is a phase of organogenesis (bud and root differentiation) during which meristematic activity is very high. This is followed by a phase of growth (rooting, flower scape elongation, and bulbing) during which cell division and/or meristematic activity are greatly reduced. Each of these phases is markedly affected by temperature. Organogenesis is promoted by the high-mean temperature sequence, while growth (scape elongation and bulbing) is promoted by the low-mean temperature sequence.

Our studies on the effects of high temperatures applied either during the end of tulip bulb enlargement or immediately after bulb harvest showed that they not only promote subsequent organogenesis but also promote the evolution of the bulb towards “physiological maturity”. A bulb must reach this stage to become reactive to low temperatures. When the bulb is not physiologically mature, a low temperature treatment cannot induce the growth processes. In addition, it appeared that a major effect of bulbs approaching physiological maturity is that the bulb reserves become readily available for subsequent growth. Thus, the degree of physiological maturity that the bulb has reached prior to being subjected to a cold treatment will affect the quality (weight) of the daughter plant. This is very important for very early forcing of the bulbs. These results indicated that the characterization of the physiological state of a bulb is very important. I was able to show

that visual degree of bud differentiation was not a good indicator, but that the duration of the period between bulb harvest and complete differentiation of its flower bud was very important. In collaboration with colleagues of INRA at Versailles, we began searching for biochemical markers.

However, even though it appeared that the evolution of free arginine in the basal plate tissues gave an indication of the physiological evolution of tulip bulbs, the results were not conclusive. With Dutch iris, we observed that the spermidine content could be an indicator of flower induction. While carrying out this research we observed that flower bulbs, which are very heterogeneous organs, must have detailed experimental designs for biochemical studies. They must be carefully defined in order to avoid any misinterpretation of the results.

When determining the relationship between bulbing and flowering not only in the tulip but also in Dutch iris, our results demonstrated that bulbing could prevent flowering under at least two situations: (1) when bulbing takes place before the completion of flower bud differentiation and (2) when bulbing starts before scape elongation occurs, i.e., when bulbs are maintained under dry conditions after a low temperature treatment or when rooting does not take place immediately after planting.

The capacity of a bulb to differentiate a flower was also investigated. With tulips, it was possible to show that bulb weight, the generally accepted dogma, was not the only factor determining that capability. The presence of active roots in the plants negatively affected flower induction in the daughter bulbs. In contrast, high temperatures applied at the end of bulb enlargement and/or immediately after harvest positively affected flower induction. With Dutch iris, dipping bulbs in a solution of ethephon promoted flower induction and subsequent flowering of small-sized bulbs.

In collaboration with Prof. August De Hertogh, I also studied the effects of scale wounding on tulip growth and flowering. We observed that an increase in ethylene concentration due to scale wounding did not result in either flower abortions or a reduction in flower scape length. It did, however, hasten flowering. These studies indicated that additional research is necessary to obtain knowledge on the roles of ethylene in tulips. It is generally considered to be a growth retardant in tulips.

The knowledge gained on the physiology of tulips and Dutch iris has been important to growers. They have a better understanding of the biological basis of bulb production and utilization. The knowledge of the effects of bulb origin as well as the consequences of bulb storage conditions on plant

growth has improved their results. The studies also clarified the causes of some of the physiological disorders observed by growers. These results have been published in scientific or technical journals and presented at ISHS Congresses over the period from 1973 to 1993. In 1983, this research received a scientific award from the Académie d'Agriculture of France.

This knowledge about the physiology of tulip was very useful to me when I initiated research on *in vitro* propagation in 1983. Initially, it was conducted in collaboration with Prof. Claude Bigot of the Ecole Nationale Supérieure d'Horticulture of Versailles and later with Prof. Jean Claude Courduroux of the University of Clermont-Ferrand. We obtained positive results by using stem discs of plants grown under dark conditions. Darkness and temperatures not higher than 20°C were very important factors for *in vitro* adventitious bud regeneration. *In vitro* bulblet production was obtained only after a cold treatment, but the results were genotype dependent. Although we were not able to develop a technique for routine *in vitro* propagation, the results obtained with some cultivars allowed us to investigate the subject of gene transfer. During this research, we observed that the gelling agent used for *in vitro* culture could affect the regeneration rate observed in the presence of selecting agents. Unfortunately, we had to terminate this research. To this day, I regret that we were not able to develop an international project on tulip *in vitro* regeneration. In order to conduct this breeding research, two factors appeared important: (1) the establishment of a large collection of cultivars and (2) the determination of their forcing ability and characteristics. We rapidly introduced over 500 cultivars (over 900 in 1980) and about 60 species. We studied their behaviour not only in the field but also in heated and non-heated greenhouses. Simultaneously, information on flower vase life was collected. These observations indicated that a great genetic diversity existed for the various characteristics of the cultivars. In addition, we found that most of the species had a poor vase-life. The results of the physiological studies were very helpful in the development of screening conditions. I was able to show that under our climatic conditions, a selection for forcing ability could be carried out when the seedlings first flower in the field. This was done by comparing their earliness of flowering and vigor to that of known cultivars.

The first crosses produced two types of results: (1) the possibility of combining plant vigor and short growth cycle appeared to be possible, and (2) the cultivars appeared to have a huge genetic variability of which only a small part had been used. The latter could partly be explained by the fact

that most of the breeding work was conducted in The Netherlands where most of the breeders probably tried to select for the same plant type. Taking this information into account, I decided to diversify the crosses. The result was the production of genetic material that combined many original characteristics, aesthetic value, and forcing ability. Since a minimum of 25 years is required before a new cultivar can be released, it is still difficult to predict the future of this material (more than 500 clones have been selected and are either being propagated or are under evaluation). When INRA decided to stop the breeding program for tulips in 1999, all the material was sold to companies responsible for their commercial development. At present, a limited number of cultivars released from the breeding program on tulips are grown on a commercial scale, mainly by Dutch companies. Among them are: Pieter de Leur, Bordeaux, Fontainebleau, and Salvation Army.

Over the years, less effort was devoted to the breeding program on Dutch iris. It has, however, resulted in some clones, e.g., 'Mount Everest' (white) and 'Blue Velvet' (dark blue), both grown commercially by Dutch and French companies.

The knowledge gained with tulip and Dutch iris was very helpful in other research projects that I either supervised or on which I collaborated. An example was the development of the in vitro propagation of Lily-of-the-Valley (*Convallaria majalis*) that was conducted in 1989. The knowledge of the effects of environmental factors on plant growth was critical for the control of plantlet regeneration in vitro. Similarly, physiological studies, based on the approach we used with Dutch iris, were very useful in the collaborative breeding program on shallots conducted by Joseph Cohat.

In addition to these major research programs, I also conducted some experiments on the early flowering of *Narcissus* and the determination of the favourable conditions for flower development of the saffron crocus (*Crocus sativus*).

Up to 1986 almost all of my time was devoted to research. In 1986, I was appointed the Director of the Research Unit and thus had to supervise the research programs devoted to potatoes and all bulbous plants. I remained in this position until 1999, when I decided to retire in December 2000.

From 1989 to 1995, I was the Chairman of the scientific and technical council of the French Comité National Interprofessionnel de l'Horticulture. This council made links between research, experimentation, extension services, and growers. Although it was time consuming, it was a very interesting experience.

In 1990, the Head of Genetics and Plant Breeding Department, asked me to coordinate all of the research devoted to ornamental plants. That led me to initiate discussions on the use of various biotechnologies for ornamental plant breeding and to encourage improved collaboration in this area. Simultaneously, I initiated discussions on the definition of original research topics in ornamental plants, as compared to agronomic crops. I also tried to convince my colleagues of the importance of collaborations with the researchers working with model plants (*Arabidopsis*).

From 1992 to 1998, I was one of two representatives of France at the Council of the International Society for Horticultural Science (I.S.H.S.).

In addition to research and administration of research, I also devoted a part of my time to the dissemination of the results of my research. Besides scientific and technical publications, I presented lectures in France at Universities, horticultural schools, extension service personnel, and growers. In addition, I was invited to speak in many other countries, e.g., Chile, Korea, and Mexico. I also had exchanges with the ARC in South Africa. However, for me, the most important mechanism for the dissemination of knowledge was the publication of the reference book "The Physiology of Flower Bulbs," published in 1993 by Elsevier Science Publishers, Amsterdam. I was much honored when Prof A. De Hertogh asked me in 1989 to be co-editor of this multi-authored book. It offered us the opportunity to update the knowledge on the biological basis of the production and the utilization of bulbous and tuberous plants. The writing and editing of this book was time and energy consuming, but provided an excellent opportunity to collaborate with numerous colleagues who shared our enthusiasm for flower bulbs.

In conclusion, I must say that I have been able to accomplish all the research that is summarized in this biography due to the fact that during my career I met many individuals whose advice and support have been very important to me. First, I thank the successive Heads of the Plant Breeding Department of INRA who provided me with the freedom to choose a wide range of research topics. During nearly 30 years I also benefited from the friendly and constructive exchanges I had with Joseph Cohat and August De Hertogh; my special thanks to them. Special acknowledgements are also due to all the efficient and loyal technicians who assisted me with my research. The confidence and the support of all these people have contributed to the enjoyment of my work. Last, but not least I acknowledge the support of my wife, Madeleine, and our four children who have given me the freedom to pursue my career. I want to thank them from all my heart and promise to give them much more time in my retirement.

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THE HAMILTON P. TRAUB AWARD FOR DISTINGUISHED SERVICE

This award was established in 2000 by the IBS Board of Directors to recognize meritorious service to the Society. It is named after Dr. Hamilton P. Traub, founder of the American Plant Life Society, antecedent of IBS, and editor of its journal for a half century.



2002 TRAUB AWARD MICHAEL G. VASSAR

My first remembrance of a geophytic plant was of some dahlia bulbs I planted when I was almost five years old. The dahlias did well, and I was impressed, and never forgot the flowers. It was years later that I found out that after I

had planted the tubers, my mother went out while I was asleep, dug up the tubers, and planted them right side up.

My grandparents had a farm with about 20 acres of fruit trees, berries, rhubarb, and many flowering trees and shrubs. I spent the summers there, learning about growing plants, and became very proficient grafting fruit trees. I also learned the value of growing plants correctly and taking care of them.

I got hooked on succulents when I was about 10 years old, and soon had to build a small greenhouse to hold over five hundred plants. In order to pay for heating the greenhouse, I grew many house plants, but most enjoyed propagating regal or Martha Washington pelargoniums.

After high school the Army got me, and I was sent to the other side of the world. But those two years, in conjunction with working in a plywood factory at night, enabled me to go to college. After getting a B.S. degree in Horticulture, I packed up my plants and books and moved to Los Angeles. I greatly enjoyed visiting the botanical gardens, and learning about a whole new world of plants.

While attending a meeting of the Gesneriad Society in Culver City, a member told me about the International Geranium Society. I joined IGS and began studying plants in the geranium family. It seemed the most interesting plants in this family had succulent stems and/or tuberous roots, which got me interested in all plants with bulbous or tuberous roots. I was soon asked if I would accept an appointment to the IGS board of directors, and served about 20 years on the board, the last 10 years as editor of their journal. After a few short jobs with plant shops, and one managing the plant department of a grocery market, I became the grower at one of the first wholesale nurseries

that rented plants and provided maintenance to offices and lobbies in large commercial buildings. From there I went to a large wholesale flower bulb company and spent 11 years as staff horticulturist and salesperson.

I left the wholesale bulb company, to begin my own company growing bulbs under the power lines in North Hollywood. I rented three acres, cleaned up all the rocks and broken glass, repaired the fence, installed an irrigation system, and planted scores of bulbs. At the end of the second year, I planted thousands each of *Sparaxis*, *Watsonia*, *Oxalis*, *Veltheimia*, *Ixia*, about 50 species of *Lachenalia*, and many more. The bulbs grew well because the soil was almost pure sand, and fast draining. Then on Christmas eve in 1990, the Yukon Express came down the west coast from Alaska, and put all of Los Angeles in the freezer. At 2 PM the temperature was 28° and by 2 AM it was 16°. Over 1000 *Veltheimia* bulbs that were 4–5 inches in diameter became mush, as everything was frozen to the ground. So little was left when the weather warmed, that it was not worth digging and sorting the few surviving bulbs.

A trip to South Africa in late summer before the freeze had yielded seeds of many new plants, and some interesting bulbs. Most of these survived in cold frames in my back yard, as I was installing heat lamps as the cold descended. Most of these new bulbs were distributed to local botanical gardens.

Because I was interested in bulbs, it was natural to visit the University of California Irvine Arboretum, where I met Harold Koopowitz. I was eventually asked by Harold if I would be interested in joining the board of directors of the International Bulb Society. It was very interesting and enjoyable working with such people as Harold, Fred Meyer, Charles Hardman, Charles Gorenstein, Alan Meerow and Elisabeth Lassanyi. After a couple of years I was asked if I would become the editor of the society's publications. I worked over 100 hours a month. I met and worked with many wonderful people, and will always be grateful for this.

For about the past four years I have been with the Huntington Library, Art Collections and Botanical Gardens, and have been the Curator of Floristic Gardens for about three years. In this position I am in charge of the Palm Garden, Jungle Garden, Subtropical Garden, Australian Garden, and Water Lily Garden. And in all of these gardens there are many interesting and unusual bulbs.

Michael Vassar died in 2002 after a long battle with cancer. His wit, enthusiasm, warmth, and service to the world of bulbs will be fondly remembered.

A REVIEW OF RESEARCH ON *CYCLAMEN*

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The genus *Cyclamen* has been the subject of several monographs since Hildebrand completed the first comprehensive treatment (Hildebrand, 1898). Despite a series of works spanning the twentieth century (Glasau, 1939; Legro, 1959; Schwarz, 1955, 1964; Schwarz and Lepper 1975; Meikle, 1978, 1984, 1989; Grey-Wilson, 1997), some fundamental questions of the phylogeny of the genus remain largely unanswered, and the delimitation of species has remained contentious. Several new species have been described since Hildebrand's work, but those species occupying a wide distribution remain poorly defined, and only the high level of endemism within the genus results in species being accurately separated.

Attempts at producing a good classification within the genus have similarly been the subject of difficulties in accurately placing species, and in the extent to which the various divisions should encompass small or larger groups of taxa. Modern volumes provide excellent reference and species descriptions, especially those of Grey-Wilson (1988, 1997), but classification remains largely subjective. Indeed, recent research has generated three phylogenies on the genus (Grey-Wilson, 1997; Anderberg et al., 2000; Clennett, 2002), which as Compton points out, cannot be a good thing for taxonomy (Compton et al., 2002).

Over the last few years there have been a series of publications in scientific journals concerning cyclamen and the family Primulaceae. Only a few of the conclusions have reached the wider horticultural audience, and there is still debate over some of the results, even in the scientific community. One of the peculiarities of taxonomy is that there is often no "correct" answer to the questions of relationships between plants. Although the rules of botanical nomenclature require that only one of a list of published names is currently valid, opinions between botanists can vary, and with them different interpretations of the evidence. For example, the spring flowering cyclamen found on Rhodes and Kos has white blooms with a pink band at the mouth of the corolla (Fig. 1). No one disputes what it is, but it has been given various names, all of which have been validly published by an author who believed the name they were using fit the facts perfectly. So we have *Cyclamen rhodium* Gorer, *Cyclamen repandum* var. *rhodense* Meikle,



Fig. 1. *Cyclamen repandum* subsp. *rhodense* growing near Kefalos on the Greek island of Kos.

Cyclamen repandum subsp. *rhodense* (Meikle) Grey-Wilson, and most recently *Cyclamen peloponnesiacum* subsp. *rhodense* (Grey-Wilson) Kit Tan. None of these names is necessarily incorrect; it's just a matter of checking the arguments each author uses to support their viewpoint and selecting the best version of the facts to use. In time, one variant always ends up in general use until new research suggests a different interpretation is needed.

The development of DNA analysis has allowed scientists to re-examine many relationships between plants. Depending on the genes chosen for examination, different degrees of separation can be looked at, so species can be separated within a genus, genera within a family, or even families within an order. Those botanists looking at plant evolution are particularly interested in the relationships of genera and families, as these can reveal how apparently unrelated plants have something in common. Primulaceae, and with it *Cyclamen*, has not escaped this research. Although in the course of writing this article, I have found that support for the new arrangement is so far confined to other researchers using DNA analysis, there is nonetheless a fundamental change that affects cyclamen now published in the literature.

A team of scientists working in Sweden has produced a series of papers dealing with relationships amongst the order Primulales (Anderberg and Stahl, 1995; Källersjö et al., 2000). Primulales contains closely related families that were the subject of this research: Primulaceae, Myrsinaceae and Theophrastaceae. An analysis of the three families based on morphology

was published in 1995, and these data were combined with DNA evidence from three gene regions in 2000. The results are surprising, and possibly a bit disturbing, for growers of cyclamen.

The superficial similarity between *Cyclamen* and *Dodecatheon* is dismissed as parallel evolution, and growers of both genera would tend to agree with that. The two have very little in common in terms of their growth, plant habit and physical appearance, as well as habitat preferences. The fact that they come from such widely separated places also supports the idea that they are only distantly related. In fact *Cyclamen* has no obvious relations in the Primulaceae, or indeed anywhere else.

The family Primulaceae consists of a number of genera, some of which show close affinities, while others are less obviously related. *Primula*, *Dionysia*, *Androsace*, *Douglasia*, *Omphalogramma* and *Cortusa* share many characteristics in common, showing a gradual change from the leafy woodland *Cortusa* and *Primula* to the highly reduced cushion species of *Androsace* and *Dionysia*. Other members of the family are more varied. *Anagalis*, *Lysimachia*, and *Trientalis* are somewhat similar, although *Lysimachia* has a huge range of variation within a single genus. Also normally included in the family are *Glaux*, with reduced petal-less flowers, *Samolus*, *Soldanella*, *Bryocarpum*, *Coris* with its unique zygomorphic (not radially symmetrical) flowers, and *Cyclamen*.

The Swedish team also looked at the members of the two related families, Myrsinaceae and Theophrastaceae. The genera in these families are all woody, varying from small shrublets to tropical trees. One genus in Theophrastaceae has many peculiarities in contrast with the majority of the family, and results suggested that it should form a new family of its own (Maesaceae).

The DNA and morphological characters produced from this work were subjected to a cladistic analysis. Generally the greater the number of individual variable characters, the better the result, and the more likely it is to stand up to close scrutiny. By using morphology and three separate DNA regions, the team believed they have strong support for the results achieved. These results break Primulaceae apart, moving many of its genera to Myrsinaceae, and *Samolus* to Theophrastaceae. Of those genera tested in the experiment, those remaining in Primulaceae consist of *Primula*, *Douglasia*, *Dodecatheon*, *Cortusa*, *Omphalogramma*, *Soldanella* and *Dionysia*. Many of the familiar genera of Primulaceae are moved to Myrsinaceae, and these include *Anagalis*, *Glaux*, *Trientalis*, *Lysimachia*, *Coris* and *Cyclamen*.

There are few similarities between *Cyclamen* and its new family, as most of the genera in Myrsinaceae are tropical trees and shrubs. Only two of these gen-

era have much of a toehold in cultivation, *Myrsine* and *Ardisia*. Both are shrubs and most of their species require heated glasshouses to grow. From a grower's point of view, they share no similarities with cyclamen (or *Lysimachia* and its relatives) whatsoever. From a bulbous plant viewpoint, however, there is little change, as *Cyclamen* was unique in Primulaceae for the presence of a tuberous rootstock, and this situation remains true in Myrsinaceae.

This is not the first case where new analysis using DNA evidence has changed the classification of plants. It is widely accepted among the scientific community that the overall appearance of a plant (its gross morphology) is often highly adapted to the circumstances under which it evolves, such as habitat, pollinator relationships or other factors. The underlying relationships may be hidden when looking at morphology alone, but are suddenly revealed by DNA. There is often greater correlation between these newly understood relationships and micro-morphology, which includes the characters of pollen, parts within the flower, surface hairs and cell shapes of the stem or leaves.

DNA work has been used to suggest relationships between species of cyclamen. However, the published results so far have used only one gene region. Stronger results come from using several genes, and, if possible, combining these with morphological characters. This is exactly the work that the Cyclamen Society has supported at the University of Reading, and initial findings are encouraging (Compton et al., 2002).

While enthusiasts may not willingly start referring to cyclamen as members of Myrsinaceae, other name changes within the genus are of more immediate interest. Recently, three changes have been proposed for species of cyclamen, and in two cases the plant reverts to an old name that has been out of favor. The third change concerns raising an infra-specific taxon to species rank for the first time.

In the "Endemic Plants of Greece, the Peloponnese," Kit Tan (2001) uses the name *Cyclamen peloponnesiacum* for the first time, separating this taxon from *Cyclamen repandum* Sibth. (Fig. 2). Hitherto this plant has been treated as a subspecies of *C. repandum*, based on the separation in geographic range and near identical morphology of the two (apart from floral color and presence or absence of splashes of pewter coloration on the leaves). There has been some evidence that separation might be considered (Gielly et al., 2001), and on that basis Kit Tan also moves the Rhodes and Kos endemic to become *C. peloponnesiacum* subsp. *rhodense*.¹

¹ Since completing this review, nomenclatural research at the University of Reading (Compton and Culham, 2003) has revised the position for *Cyclamen repandum*. As discussed, there have been several names published for taxa in this group. It is now clear that under the rules of priority, if the spring



Fig. 2. *Cyclamen peloponnesiacum* growing south of Githio in southern Greece.

Detailed studies of DNA by a team at the University of Reading have begun to highlight some new factors on the relationships within *Cyclamen*. *Cyclamen repandum* was separated, in their analysis, from *C. peloponnesiacum*. Kit Tan. *C. peloponnesiacum* grouped with *C. creticum* whilst *C. repandum* grouped with *C. balearicum*. The relationships among these taxa are to be the subject of further investigation, and at present the data from Reading suggest that the new species proposed by Kit Tan (2001) might be legitimate. However, the team believes that further evidence is needed to fully warrant acceptance of the change, and that this might resolve the questions regarding all the species within this group (Schwarz' subgenus *Psilanthum*). More surprisingly, considering current classification, is the grouping of *C. cyprium*, *C. libanoticum*, *C. pseudibericum* and *C. parviflorum*. The support for this grouping is good. Substantial variation is evident among the *C. hederifolium* samples sequenced so far at Reading. This level of variation is equivalent to that seen across the whole of subgenus *Psilanthum*, suggesting an inconsistent species concept within *Cyclamen*. It is therefore possible that there are further infraspecific taxa to be recognised within *C. hederifolium* as work progresses.

The case of a name change to that tongue twisting species from south west Turkey is rather different. When Professor Otto Schwarz published the name of *Cyclamen trochopteranthum* in 1975 (Schwarz and Lepper, 1975),

flowering plants in the Greek Peloponnese and Rhodes are recognised as separate from *C. repandum*, they should be assigned to *C. rhodium* Gorer on Rhodes, and to *C. rhodium* subsp. *peloponnesiacum* (Grey Wilson) J. Compton and Culham on mainland Greece.

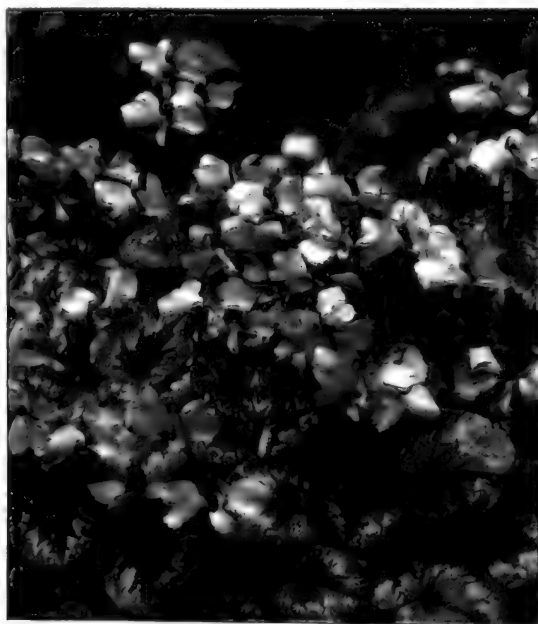


Fig. 3. *Cyclamen alpinum* in cultivation in England.

he did so based on his opinion of evidence at the Berlin Herbarium. Schwarz studied the information available to him in detail, and believed that all references to the name *Cyclamen alpinum* were at most variants of *C. coum*. Two separate authors had in fact published the name of *C. alpinum*, Sprenger in 1892 and Hildebrand in 1898. The Berlin Herbarium lost all the relevant material in the Second World War, so no one today can verify what the plants actually were. However, Hildebrand's monograph contains detailed descriptions and line drawings of the plants he studied. When I was researching at Reading University in 1995-7, I was fortunate to examine closely an original copy of Hildebrand's monograph, and my opinion at the time, based on the line drawings and the very little German I can read, was that Hildebrand's *Cyclamen alpinum* was identical with the plants grown now as *C. trochopteranthum*. At the time I felt unable to proceed on this basis, but Grey-Wilson (2002) has now done so, following the publication of the Cyclamen Society's translation of Hildebrand, which demonstrates that the two species are identical. Strictly speaking, Sprenger's use of the name predates Hildebrand. However, this is not a unique situation, and Grey-Wilson produces supporting arguments that the original publication was also of this species. So *Cyclamen alpinum* hort. Dammann ex Sprenger reappears as the oldest published name for this plant (Fig. 3).

The variation within *Cyclamen coum* has long plagued growers and taxonomists alike. Recent work, including my own, suggests the populations from Iran should be separated as a different species. The name they come under is not new, as these plants were initially described as a species in 1860. It is only now that on balance we support that particular interpretation, and *Cyclamen elegans* Boiss. & Buhse reappears in the literature, adding an extra species to our list.

My own research involved detailed morphological studies carried out on plants in cultivation, and on herbarium specimens. In addition, phytochemical examinations of leaf flavonoids were carried out on a small sample of species and the collected data used to complete cladistic and phenetic analyses of the genus (Clennett, 2002). Because of a particular interest in *Cyclamen coum* and its relatives, the most detailed examinations were carried out on Schwarz' subgenus *Gyrophoebe*. This comprises *C. coum*, *C. alpinum*, *C. parviflorum*, *C. elegans*, *C. mirabile*, *C. cilicium*, *C. intaminatum*, *C. pseudibericum*, *C. libanoticum* and *C. cypricum*. Studies of the micro-morphology of cyclamen pollen proved very interesting, separating most of the species in this subgenus from the rest of the taxa by the number of apertures possessed by each pollen grain (Clennett, 1999). Virtually all the species of *Cyclamen* have three apertures and are 3-colporate grains. However, with the exception of *C. cypricum* and *C. libanoticum*, all those within subgenus *Gyrophoebe* have four apertures (4-colporate). Two species, *C. pseudibericum* and *C. parviflorum*, have both three and four apertures present in different pollen grains. *Cyclamen coum* and *C. elegans* have both four and five aperture grains present. The percentage of 5-colporate grains is small in *C. coum*, but up to 50% in *C. elegans*. While cladistic analysis of *Cyclamen* morphology separated *C. libanoticum* and *C. cypricum* from the rest of the subgenus (moving the pair to subgenus *Cyclamen*), the pollen analysis supports grouping these two species with *C. pseudibericum* and *C. parviflorum* as found in the recent DNA studies at Reading.

Publication of the research work I completed at the University of Reading (Clennett, 2002) produces a new phylogeny for *Cyclamen* from morphology alone. Support for the classification proposed was good for the majority of relationships, but there were some weaknesses in key areas. Evidence from Reading with DNA now suggests this might lead to changes in some details, which has also been a problem with several of the recently proposed classifications of the genus. The classification is therefore not republished here.

A separate phenetic analysis of taxa in subgenus *Gyrophoebe* graphically showed the closeness of relationships within this group. As might be expected,

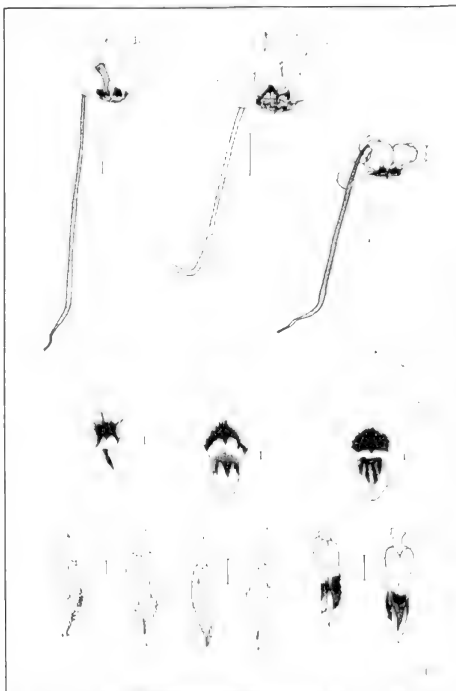


Fig. 4. Morphological comparison. Entire flowers of A: *Cyclamen coum*, B: *C. elegans* and C: *C. alpinum* (scale bars 10mm). Individual petals of D: *C. coum*, E: *C. elegans* and F: *C. alpinum* (scale bars 1mm). Lateral and ventral views of stamens G: *C. coum*, H: *C. elegans* and I: *C. alpinum* (scale bars 1mm).

C. cyprium and *C. libanoticum* once again appear more distinct from the remaining species, with *C. pseudibericum* also well separated. All the remaining species are evidently close, but they appear in ordinal analysis as distinct clusters and are thus supported as separate entities. Using this analysis, *C. coum* and *C. elegans* are as well defined as the other recognised species, and thus deserve separation as species in their own right.

Several morphological and micro-morphological differences separate the two species (Fig. 4). These include leaf shape (*C. coum* has reniform leaves largely devoid of broad marginal scalloping, while *C. elegans* has ovoid leaves coming to a distinct distal point and obvious scalloping of the

margins). There are also differences in the positioning of the marginal hydathodes. The shape and vein patterning of calyx lobes also differs markedly, with *C. coum* having sepals visibly without veining, whereas in *C. elegans* the sepals show three distinct veins on the exterior. The corolla is a very obvious distinguishing character. In *C. coum* the petals are short, often no longer than wide, and obtuse at the tip. At the base there is a darker region within which are two "eye" spots which are usually white, regardless of the main color of the petal. In *C. elegans* the petals are longer, come to a distinct point at the tip and bear self colored "eye" spots at the base. Within the flower a separate dark mark extends into the corolla tube. This is a single broad line in *C. coum*, but a three pointed "M" shape in *C. elegans*. On the style there is a distinct constriction behind the stigma in *C. coum*, which is absent in *C. elegans*. The anthers differ in the shape of the dorsal papillae, which are short and indistinct in *C. elegans*, but long and prominent in *C. coum*. The type and size of epidermal trichomes also varies between the two species. The shape and size of the abaxial epidermal cells are

also different in the samples examined, but variation between specimens in other taxa was observed, and this may not be a reliable character.

Since virtually all the taxa of the subgenus are Turkish endemics, geographical isolation within pockets of suitable habitat would appear to give the best explanation of speciation within this part of the genus as a whole. The obvious exception here is *Cyclamen coum* s.l. which has a wider distribution from the Ukraine, Georgia and Bulgaria to the north, in a broad band round the western, southern and eastern shores of the Black Sea, with the additional separate areas to the south from Turkey through Lebanon and Syria to Israel. Also separated are the isolated populations on the south Caspian coast in Iran (Wendelbo, 1965).

Small but significant morphological and micro-morphological differences separate this Iranian taxon from the other variants of *Cyclamen coum*, so re-instatement of this plant at species level is justified by the results obtained. It thus becomes *Cyclamen elegans* Boiss. & Buhse. The similarly isolated taxon in south Ukraine, found only in the Crimea, has been separated by Russian taxonomists (Pobedimova, 1952) as *C. kusnetzovii* Kotov & Czernova. Material of this plant is extremely scarce in cultivation and only one specimen of unknown origin was available for study. At the time of these experiments, this individual had not produced flowers and the only distinguishing features were the much smaller than usual leaf lamina and semi-evergreen habit. Subsequently, flowers have been produced, but aside from their small stature they are not significantly different from those of *C. coum*, and separation at the specific level therefore seems inappropriate without further study.

Field studies by the Cyclamen Society (Wood, 1990, 1991) and others (Brickell, 1979; Grey-Wilson, 1997; Meikle, 1984, 1989) have shown a clinal pattern of variation in *Cyclamen coum*, and some of the characteristics seen in *C. elegans* become gradually apparent in the eastern extremes of *C. coum* subsp. *caucasicum* (K.Koch) O.Schwarz. The phenetic analysis used here confirms this finding, with some individuals of *C. coum* from the eastern extremes of its range positioned close to the group of *C. elegans*. However, there exist sufficient distinctions to warrant separation of these two taxa at the specific level, although further study into the distribution of *C. elegans* is obviously merited.

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A REMARKABLE NEW DISCOVERY IN *CLIVIA*

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Clivias are striking flowering plants. Most people know them best in cultivation, either as venerated old pot plants or as beautiful shade plants in lush, well kept gardens. None of these settings, however, manages to saturate the senses as do *clivias* in nature—wild, wooded places mostly in the subtropical eastern region of southern Africa. The climate along the eastern seaboard is equable, the rain falls in summer and the atmosphere is humid for several months of the year. Under these conditions southern Africa's best-known *Clivia* species, the highly prized *C. miniata*, occupies scattered sites from Eastern Cape to Mpumalanga. It shares parts of its geographic range with three other species of the genus. *Clivia nobilis* is found in the southern-most part near East London and Grahamstown, Eastern Cape, whereas *C. gardenii* is more widespread and extends from northern Eastern Cape, through Kwazulu-Natal to Swaziland (Pooley, 1998). *Clivia caulescens* occupies the northern-most areas in Mpumalanga and Limpopo Province. The genus has two distinct floral forms. The erect, trumpet-shaped flowers of *C. miniata* that glow orange in the dappled sunlight attract swallowtail butterflies, whereas the hanging, reddish, tubular-shaped flowers of the other species are visited by sunbirds. Natural hybrids between *C. miniata* and the tubular-flowered species are known but they are rare in the wild.

Botanical exploration in South Africa began in the 17th century and plant collecting has been actively pursued for the past 150 years. Consequently, *clivias* in southern Africa are well known plants and few people ever imagined that an undescribed species was yet to be found. Needless to say, the discovery, little more than a year ago, of *C. mirabilis* (Rourke, 2002) from the semiarid Northern Cape Province (Fig. 1)—approximately 600 km north west of any other known *Clivia* species—came as a huge surprise. The whereabouts of the new species is such that growers and botanists cannot overlook the need to reassess the horticultural potential and evolutionary history of the genus.

The species first came to the attention of botanists early in 2001, when Mr. Wessel Pretorius, Officer in charge of the Oorlogskloof Reserve, 350 km north of Cape Town, sent pressed specimens to the Compton Herbarium to be identified for a checklist of the area. After careful field studies, Dr. John Rourke, Curator of the Compton Herbarium described *C. mirabilis* formally in May 2002.

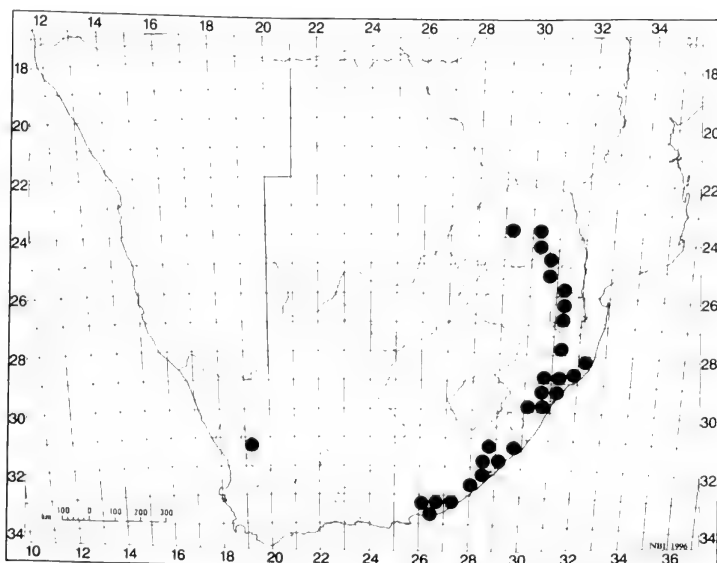


Fig. 1. The current distribution of *Clivia* in southern Africa.

Oorlogskloof, a 100 m deep gorge, lies on the Bokkeveld Escarpment close to Nieuwoudtville in an area well known for its wildflower displays (Snijman and Perry, 1987). Sheer sandstone cliffs and huge tumbled rocks and screes (Fig. 2) make access to the gorge difficult except along a hiking trail recently laid out by the Northern Cape Directorate of Environmental Conservation. Winding its way southwards along the valley bottom, the Oorlogskloofrivier is reduced to a narrow stream interspersed with rock pools in summer, only to become a strongly flowing current in winter. Succulents such as species of *Aloe*, *Cotyledon* and *Tylecodon* cover the hot, dry north east-facing slopes, whereas the moister and cooler south west-facing slopes provide occasional shade for patches of lightly wooded thicket, made up mainly of species of Celastraceae. These rocky, dappled sites are home to scattered clumps of *C. mirabilis*.

In general appearance the habitat of *C. mirabilis* is similar to that of *Clivia* species in the east of southern Africa but it is much harsher. The mean annual precipitation at Nieuwoudtville is approximately 350 mm, whereas in the east the habitats for *C. nobilis* around Grahamstown receive 300 to 600 mm rain per year. In other respects, however, the climatic gradient in the Cape from west to east shows significant differences. Rain falls in winter (between April and September) in the west, which contrasts with a bimodal regime (spring and autumn) in the east. Moreover, solar radiation



Fig. 2. Oorlogskloof in Northern Cape, South Africa.

drops by 15% from west to east, seasonal and diurnal temperature ranges are greatest in the west, and evaporation is about 40% higher in the west, particularly in summer (Deacon et al., 1992).

Clivia mirabilis is most similar to *C. nobilis*. The channeled, leathery leaves, which reach 0.6 to 1.2 m long, grow in a basal cluster from a short underground rhizome anchored by long, fleshy roots. With light shining from behind, the leaf margins appear pale and a whitish stripe sometimes runs down the midrib to a reddened base. The blades, however, lack the distinctive apical notch and minute marginal serration found in *C. nobilis*. From October to November the plants produce a 30 to 80 cm long scape that carries 20 to 48 pendulous, tubular flowers, in which the tepals are 35 to 50 mm long and fused at the base for 10 to 15 mm. The perianth is scarlet with yellow tips and is made all the more striking by the red pedicel and ovary (Fig. 3). Malachite sunbirds and lesser double collared sunbirds visit the flowers for nectar and seem to be the likely pollinators. Within six months of flowering, large, irregularly shaped, vermilion fruits develop, sometimes with as many as 25 to 35 berries in each cluster. Each fruit has several 10 mm wide, non-dormant seeds, which are pearly white when mature.

Mr. Graham Duncan, who has grown clivias at Kirstenbosch Botanic Garden for many years, has found that seed of *C. caulescens* and *C. nobilis* mature quite quickly, within six to eight months. Thereafter the seedlings



Fig. 3. *Clivia mirabilis* in habitat.

grow slowly and eventually become long-lived individuals (Duncan, 1999). This habit suggests that plants of the closely related *C. mirabilis* are equally long-lived and that the population itself has a long history.

To understand how *C. mirabilis* became isolated in the north western Cape it is necessary to ask why clivias are unknown in the intermediate southern and south western Cape, despite the presence there of what appear to be suitable habitats for their growth. That clivias may yet be discovered in the south certainly cannot be ruled out. But since plant collecting in the Cape has been more intensely pursued than elsewhere in southern Africa, it is reasonable to expect—if clivias do indeed exist in the south—that collectors would have recorded such large evergreen plants by now.

If the gap in the geographic distribution of *Clivia* is real, however, then two possible scenarios may account for this unusual distribution pattern. Either the widely separated Oorlogskloof population was established relatively recently through long distance dispersal or it is an ancient remnant of a once widespread ancestral species.

Observations that wild clivias occasionally grow in the forks of trees (Duncan, 1999) suggest that vectors like birds or monkeys may indeed carry the seed for short distances. However, vervet monkeys do not extend into the south-western or north western Cape and no frugivorous birds are known to migrate between the eastern and north western Cape (Peter Steyn, pers. comm.). Thus, it seems highly unlikely that the isolated *Clivia* population at Oorlogskloof is the result of a chance long distance dispersal event.

Scientists know enough about the origins of the Cape Region—the floristic area between Nieuwoudtville, the Cape Peninsula and Grahamstown—to tell something of its biological history. Fossil evidence indicates that 60 million years ago conditions in the Region were generally warm, wet and tropical, and great forests covered the area. By about five million years ago conditions were relatively dry and cool, and the climate began to resemble the mediterranean-climate of today. The forest began to retreat and there is evidence that fire had become an important ecological factor. A further drying of the climate three million years ago resulted in the virtual elimination of forest as the treeless, fire-swept landscape of the fynbos was born (Cowling and Richardson, 1995). In particular, there is good evidence that the incidence of frequent, high-intensity fires resulted in the extinction of many Tertiary forest lineages in the Cape Region (Cowling et al., 1996).

It is significant to note that many genera of Amaryllidaceae are richly represented in the fynbos of the Cape Region and that the plants cope well with the challenges of fire. In fact several species of *Cyrtanthus* and *Haemanthus* actually depend on fire to flower. However, unlike their fire adapted relatives, clivias—with their evergreen habit and lack of a storage bulb—are ill equipped to survive intense fire and this factor may have served as an isolation mechanism. Under this assumption it seems most likely that *C. mirabilis* has persisted at Oorlogskloof for hundreds of generations, untouched by the fires that destroyed its ancestors that occupied the Cape during more favorable times.

Clivia mirabilis is without doubt an aptly named species, whose survival in the remote Oorlogskloof, Northern Cape is truly to be marveled at. As hardy survivors, these plants rightfully deserve our deepest respect.

ACKNOWLEDGEMENTS

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THE SYSTEMATIC VALUE OF NUCLEAR DNA CONTENT IN *CLIVIA*

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Abstract. Genome size (Cx-value) was applied as a new criterion to investigate the relationships within the genus *Clivia* Lindl. (Amaryllidaceae). Samples representing all 5 published species, and a sixth yet unnamed taxon ('Robust Gardenii') were investigated. The species of *Clivia* have the same basic chromosome number ($2n = 2x = 22$). However, the somatic nuclear DNA contents (2C), as measured by flow cytometry with propidium iodide was shown to range from 31.2 to 39.2 pg. *C. miniata* and *C. caulescens* turn out to have nearly the same total nuclear DNA content, and the same is true for *C. gardenii* and *C. 'Robust Gardenii'*. If low DNA content is anything to go by, then *C. mirabilis*, having the lowest DNA content, could be the most primitive species. Arranged according to a decreasing DNA content, a reversed order is reached compared with the total length of the karyotype as published earlier. A difference of 8 pg in nuclear DNA content implies that the largest genome contains 8×10^9 more base pairs than the smallest and has chromosomes that are 30% larger. Flow cytometry is applicable even in the case of non-flowering plants, and therefore has applications in conservation monitoring and the determination of the results of interspecific crosses. The classical taxonomic traits based on morphology and the available molecular data are here supplemented with data on nuclear DNA content.

INTRODUCTION

The genus *Clivia* Lindl. (Amaryllidaceae) now comprises 5 described species and a yet undescribed sixth taxon that occur naturally in South Africa only. *Clivia nobilis* Lindl. was the first to be described in 1828. *C. miniata* (Lindl.) Regel, was described in 1853, differing in its open, not tubular, flowers. It is the species most often encountered in culture. Several cultivars are described, including one with yellow instead of orange-red flowers. In 1856 another species with tubular flowers, *C. gardenii* Hook. was described, followed in 1943 by *C. caulescens* R.A. Dyer. Ran et al. (2001) point to a possible fifth species (colloquially known as 'Robust Gardenii', or 'swamp clivia') also having tubular flowers, but differing in DNA sequence. It also grows in wet places contrary to the others, which grow in shady, rocky places. Great

was the surprise when in 2001 another species was found 800 km to the west. It is not only far removed from the other species, but grows at least part of the day in full sun (Rourke, 2002).

Clivias are popular plants both for indoors or outside in more favorable climates. All species are in cultivation. The tubular-flowered taxa that are in culture are often confused. All species counted have the same chromosome number, $2n = 2x = 22$.

By doing a karyotype analysis and studying the sequences of two nuclear genes, Ran et al. (1999, 2001a, 2001b) have substantially clarified systematic relationships within *Clivia*. However, *C. mirabilis* was not available to them at that time. To elucidate the relationships between all 5 (6) *Clivia* species, characters were investigated that were not used previously. Nuclear DNA content was measured in all five recognized species and the 'Robust Gardenii' by flow cytometry with propidium iodide. The classical taxonomic traits based on morphology and the available molecular data are here supplemented with data on nuclear DNA content.

Nuclear DNA content. Nuclear DNA content, which can conveniently be measured by flow cytometry using propidium iodide (PI), a stoichiometric DNA stain that intercalates in the double helix, has seldom been exploited for taxonomic purposes. Where species in a genus have the same chromosome numbers, differences in nuclear DNA content, when present, have proven to be very effective in delimiting infrageneric divisions in a number of taxa (Ohri, 1998). PI flow cytometry can therefore be considered as a quick and useful method for understanding systematic relationships. Genome size has been demonstrated to vary between taxa with identical chromosome numbers (Ohri, 1998; Zonneveld and van Iren, 2001; Zonneveld, 2001). Moreover, Greilhuber (1998) has clearly shown that intraspecific variation of genome size is much less than assumed. Flow cytometry was successfully used to measure the $2C_n$ -value for the genera *Hosta* (Zonneveld and van Iren, 2001), *Helleborus* (Zonneveld, 2001), *Galanthus* (Zonneveld et al., 2003) and *Agapanthus* (Zonneveld and Duncan, 2003).

MATERIALS AND METHODS

Plant material. Plant material was obtained from the collection of K.R.W. Hammet via B.G. Murray, and the recently described *C. mirabilis* Rourke was obtained from the author of that species, J.P. Rourke. Where possible, we used material of known wild origin.

Flow cytometric measurement of nuclear DNA content. For the isolation of nuclei, about 0.5 cm² of adult leaf tissue was chopped together with a piece of *Agave americana* L. as an internal standard (see below). The chopping was done with a new razor blade in a Petri dish in 0.25 ml nuclei-isolation buffer to which 0.25 mg RNase/ml was added (Zonneveld and van Iren, 2001). After adding 2 ml propidium iodide (PI) solution (50 mg PI/l in isolation buffer) the suspension with nuclei was filtered through a 0.0-3 mm nylon filter. The fluorescence of the nuclei was measured half an hour and one hour after addition of PI, using a Partec CA-II flow cytometer. The optical path contained a HBO mercury lamp, filters KG1, BG12, dichroic mirror TK500, filter OG570 and a Leitz 50 x 1 water immersion objective. Data were analyzed by means of DPAC software (Partec GmbH). The 2Cn DNA content [in picograms, (pg)] of the sample was calculated as the sample peak mean, divided by the *Agave* peak mean, and multiplied with the amount of DNA of the *Agave* standard. At least seven different samples, and at least 5000 nuclei, were measured twice for each clone. Most histograms revealed a Coefficient of Variation (CV) of less than 5%. The standard deviation was calculated for the DNA content of each species, using all relevant measurements.

Internal Standard and absolute DNA content values. When measuring nuclear DNA content by means of flow cytometry, it is necessary to chop tissue from the plant of interest together with an internal standard: this standard must be as close as possible to the plants of interest. In this way, variation in signal intensities due to staining kinetics, to light absorption and quenching by sample components, as well as to instrument and other variables, is reduced to a minimum. *Agave americana* L. was chosen as internal standard, because it has a convenient amount of DNA compared with *Clivia*. Moreover, *A. americana* is available year-round, does not mind several weeks without water and, being a large plant, it can serve numerous determinations, thereby further reducing variation in readings. It also has a low background in PI measurements, and shows a single G₀ peak, almost lacking G₂ arrest. Fresh male human leucocytes (2Cn = 7.0 pg, 1pg = 10⁻¹² gram) were chosen as primary standard (Tiersch et al., 1989). This yields 2Cn = 15.9 pg for somatic nuclei of *A. americana*.

RESULTS AND DISCUSSION

Genome size. All known *Clivia* species were investigated experimentally by flow cytometry, a method not previously applied to *Clivia*. Genome size as

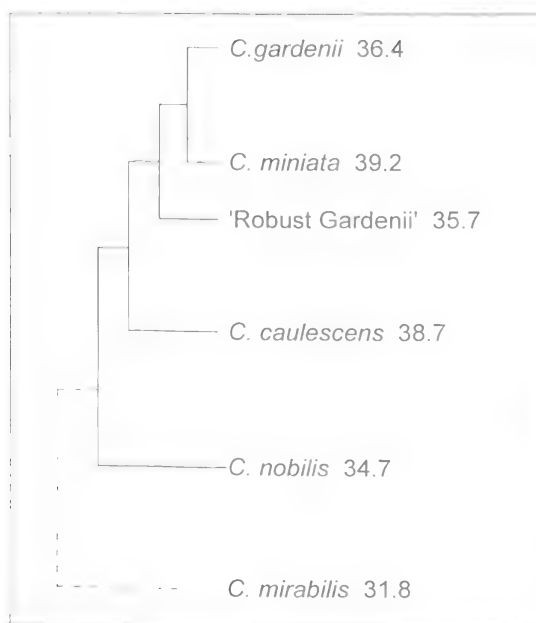


Fig. 1. Phylogenetic tree of *Clivia* species redrawn from Ran et al. (2001b) with nuclear DNA contents listed.

investigated here (see Table 1), complements the work based on karyotype analysis and gene sequencing (Ran et al., 1999, 2001a, 2001b). Taxa clearly different in nuclear DNA amount are considered good species. This does not mean that taxa with identical DNA amounts must always be considered as constituting a single species. The nuclear DNA amounts should always be evaluated in combination with morphological/molecular data, just as any other taxonomic characters. The species are listed according to a decreasing nuclear DNA content (Table 1). The interspecific variation shows that genome size in *Clivia* varies between 31.2 and 39.2 pg (Table 1).

Relationships between *Clivia* species cannot be inferred using DNA amount values alone. However, the DNA values are very close overall suggesting that they are strongly related. This is also indicated by the fact that most species are cross compatible and produce fertile progeny (Hammett, 2002). In particular, the DNA content of *C. gardenii* and 'Robust Gardenii' with 35.7 and 36.4 pg are nearly identical. This suggests that they may be the same species and that 'Robust Gardenii' is at most a variety of *C. gardenii*, also indicated by their low sequence variation for the ITS and the 5S rDNA regions (Ran et al., 2001b). However, *C. caulescens* and *C. miniata*, with 38.7 and 39.2 pg

respectively, are also nearly identical in DNA content but this is not substantiated by their place in the phylogenetic tree (Fig. 1). There *C. miniata*, *C. gardenii* and 'Robust Gardenii', with an overlapping geographic distribution, are closely related.

The difference between the highest and lowest DNA contents is 8×10^9 base pairs. This difference in DNA content must be the result of a vast number of genomic changes. Repetitive DNA elements, including retrotransposons, are major components of eukaryotic genomes and such elements have a tendency towards amplification (Bennetzen and Kellogg, 1997). Major decreases in genome size occur less frequently, and such decreases have been observed especially following a doubling of the total genome by polyploidization (Ohri, 1998), or the change from perennial to annual habit (Bennett, 1972). The phylogenetic tree (Fig. 1) redrawn from Ran et al. (2001b), is given for all species with their nuclear DNA content. The nuclear DNA amounts for *Clivia*, presented in a decreasing order, do not coincide with the phylogenetic tree published by Ran et al. (2001b). *Interestingly, the phylogenetic tree based on chloroplast DNA sequences of Conrad and Reeves (2002) resolves the same relationships supported by our DNA content.

Clivia nobilis was considered to be the most basal species in the phylogenetic tree (Ran et al., 2001b). This conclusion was also reached by studying RAPDs (Ran et al., 2001c). *C. nobilis* has, at the same time, the lowest DNA content of the 5 species investigated (*C. mirabilis* was not available to them). It is shown here that *C. mirabilis* has an even lower DNA content, suggesting that *C. mirabilis* can be considered as the most basal species. Tentatively its place in the tree is indicated here. Further molecular analysis is needed to reveal whether *C. mirabilis* with a nuclear DNA content of only 31.2 pg is indeed the most primitive. Moreover, the sequence of species in the phylogenetic tree, compared with their DNA contents as shown above, seem to indicate that both increases and decreases in nuclear DNA content have contributed to karyotype evolution in *Clivia*. It cannot be excluded that this increase and decrease in DNA content is related to old hybridization events.

In Table 1 we also have collected some data from Ran et al. (1999). It is remarkable that the total karyotype (or chromosome length) is inversely proportional to the amount of nuclear DNA in the species. A direct correlation was to be expected, as chromosome length is directly related to nuclear DNA content. The large difference in heterochromatin content reported (Ran et al., 1999; Table 1) seems not to be reflected in the amount of

nuclear DNA found here.

An alternative “tree” could be made, placing the species with the highest amount of nuclear DNA at the “top”, although DNA quantities alone are not usually used in phylogeny reconstruction. In that case, compared with the original tree (Fig. 1), only *C. caulescens* would have to change place with *C. gardenii*. Then *C. miniata* and *C. caulescens* with nearly identical DNA amount (39.2 and 38.7 pg respectively.) would be close together, as would *C. gardenii* and the ‘Robust Gardenii’, also with nearly identical amounts of DNA (36.4 and 35.7 pg, respectively). *C. nobilis* and *C. mirabilis* would keep their place at the base with 34.7 and 31.8 pg respectively. We could even go a step further and suggest that there are actually only four species. This can be done, based solely on their amount of DNA, by considering *C. caulescens* as a subspecies of *C. miniata* and ‘Robust Gardenii’ as a subspecies or var. of *C. gardenii*! However this alternative is rather speculative, to say the least, and not substantiated by the DNA sequencing results.

Grime and Mowforth (1982) suggested that in dry, growth-limited situations, species adapt over evolutionary times with an increase in DNA content. The opposite occurs in permanently wet situations. This was confirmed for *Hosta* (Zonneveld and van Iren, 2001), but is not found here in *Clivia*. *C. mirabilis*, growing in the driest conditions of all *Clivia* species, does not have the highest nuclear DNA content, nor does ‘Robust Gardenii’ or “Swamp Clivia” have the lowest.

The speed and cost effectiveness of measuring nuclear DNA content and its predicative accuracy makes it useful as a tool for identifying the vulnerable species *C. mirabilis* (see also Ran et al., 2001a). In some cases, the measured DNA value gives rise to questions about the perceived taxonomic relationship of certain taxa, which are identified as requiring further investigation. Flow cytometry is shown here to be a useful tool to indicate the taxonomic status of *Clivia* clones.

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Table 1. Nuclear DNA amounts in *Clivia* species.

	DNA in pg	Karyotype Length*	Heterochromatin*
<i>C. miniata</i>	39.2 +/-0.3	238	9.8%
<i>C. caulescens</i>	38.7 +/-0.4	244	1.6%
<i>C. gardenii</i>	36.4 +/-0.2	258	7.9%
<i>C. 'Robust Gardenii'</i>	35.7 +/-0.3	--	--
<i>C. nobilis</i>	34.7 +/-0.4	281	4.9%
<i>C. mirabilis</i>	31.2 +/-0.2	--	-

* Data from Ran *et al.*, 1999

THE ECOLOGY AND CULTIVATION OF TERRESTRIAL ORCHIDS OF ARGENTINA

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ABSTRACT

A study of the ecology and culture feasibility of 9 species of native orchids from Argentina: 2 belonging to the genus *Sacoila*, 1 species of *Skeptrostachys*; 1 species of *Pelexia*; 3 species of the genus *Habenaria* and 2 of the genus *Chloraea* were performed. The individuals were cultivated in the City of Buenos Aires from propagules or adult plants in pots with soil from the collection sites. The production of aerial and reproductive stems, as well as storage organs, was observed. The watering was managed according to the climatic conditions of the collection place. After at least one period of growth the adaptation to culture was evaluated. The species under study live in different ecosystems from forests to grasslands. Most of the species responded positively to their cultivation in containers. We discuss the possible use of these species for gardening, the suitable conditions for their cultivation and the importance of the data obtained in the ex-situ conservation of these terrestrial orchids.

INTRODUCTION

The Orchidaceae are terrestrial, epiphytic, or saprophytic herbs comprising one of the two largest families of flowering plants with about 1,000 genera and 15-20,000 species. In Argentina ca. 200 species of orchids, distributed in 41 genera, can be found in subtropical and temperate areas in different kind of environments (Dressler, 1993; Johnston, 2001).

Most of these species are perennial, emerging each season, reproducing, and then entering dormancy at the end of the season. These plants have evolved specialized requirements in their habitats. Each orchid species will germinate and grow only when these requirements are optimal. Orchids are also unique in their methods of fertilization, seed production, germination, and pollination strategies. Due to the symbiotic relationship between orchid and fungus (mycorrhizae), many orchids can remain underground for many years, building food reserves and energy to commence flowering and reproduction. After this large expenditure of energy, the plant will return

underground for several more years. During this underground phase, the orchid survives using food and energy provided from its mycorrhizal symbiont. The orchid will re-emerge when nutrient reserves are sufficient for another attempt at reproduction. This underground phase explains why many orchid species are not found in the same place from year to year. Because the evolutionary path of orchids is long, each species has had the time to adapt to a specific niche in the environment. Each species is typically associated with a specific set of habitat conditions such as nutrient availability, sunlight, and water. The low plasticity of orchids may be the result of the specific conditions needed to form the mycorrhizal association mentioned above. Because some orchids are considered mid-successional species and compete poorly with other vegetation, some species actually respond positively to certain disturbances, such as fire (Gleason and Cronquist, 1991).

The introduction of potential new ornamental crops includes the study of their biology, developing crop production, propagation techniques, and breeding improved cultivars. There is very little information about terrestrial orchids cultivation, so the main goal of this research is to obtain the specific cultural requirements such as temperature, water, and other needs of terrestrial orchids from Argentina.

MATERIALS AND METHODS

From 1996 to 2002, adult individuals or propagules of terrestrial orchids from different locations in Argentina were collected and identified, if possible, to species using available references (Williams, 1939; Correa, 1950; Johnson, 2001). Plants were cultivated in pots containing soil from the collection place and sterilized substrate. Repotting was performed in the same way with special care to keep part of the original substrate. The plants were grown under controlled conditions in a greenhouse in the Faculty of Agronomy, University of Buenos Aires. The watering was restricted completely during the underground period, according to the climate conditions in the area of origin. The species from Patagonia (*Chloraea magellanica*) remained in a refrigerated area of the greenhouse (with temperatures near 7° C day and night) for 60 days. No additional lighting was provided. Vegetative, reproductive, and storage organ development were observed. A hardiness zone map for South America based on that of the USDA (Cathey, 1990) can be found in <http://www.plantideas.com/zone/sazone.html>. We used this zone map and created a hardiness index according to how difficult it is to cultivate them in our local conditions. Index values range from I = difficult to V = easy.

RESULTS

In Table 1 (page 54) can be found the origin, the habitat and the kind of soils where the plants were found. Most of the species live in open areas like grasslands or wetlands in north and central Argentina. *Sacoila lanceolata* and *Habenaria gourleana* have the broadest distributions in Argentina, and have been cited in 17 and 16 provinces of Argentina respectively. *S. lanceolata* is very common but *H. gourleana* can only be found in wet sandy soils in small populations.

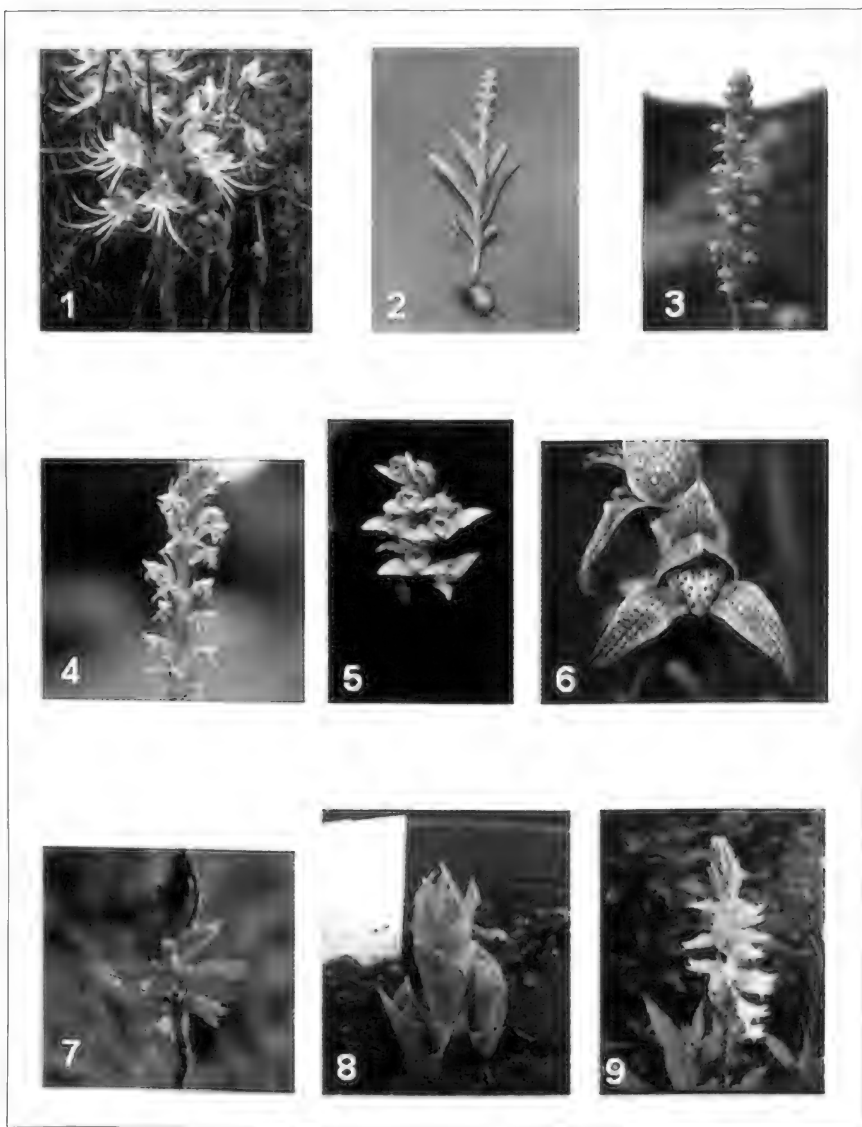
SPECIES STUDIED

Habenaria gourleana. Perennial herb from 50 to 80 cm tall, growing from fleshy tubers; the roots are long and fleshy. The flowers are white, grouped in a raceme, fragrant especially during the evening, with a 13 cm long spur protected by the bracts. This species occurs in wet sandy soils in north and central Argentina. Flowers are visited by nocturnal moths (Galetto et al., 1997). Under culture the stems sprout in October, produce flowers during January and dry down in March. Watering must be completely suppressed from April to September. Zone 9A, 9B; Index I. (Fig. 1).

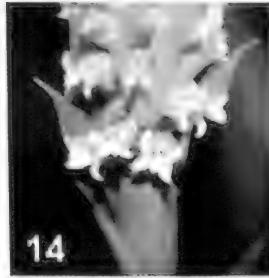
Habenaria hyeronimii. Perennial herb from 20 to 30 cm tall, growing from fleshy tubers. The flowers are green with a short spur and are grouped in a raceme. This species occurs in sandy soils in central Argentina. Under culture the stems sprout in October, produce flowers during January and February, and dry down in March. Watering must be completely suppressed from April to September. Zone 9A, 9B; Index I. (Figs. 2, 3)

Habenaria parviflora. Perennial herb from 30 to 40 cm tall, growing from fleshy tubers. The flowers are small and green with a short spur and grouped in a raceme. This species occurs in wet soils in northern Argentina. Under culture the stems sprout in September, produce flowers during December to January, and dry down in March. During the rest period watering should not be suppressed. Zone 10 A; Index III (Fig. 4).

Chloraea membranacea. Perennial herb from 40 to 50 cm tall, with fleshy roots. The flowers are white, grouped in spikes, and visited by halictid bees. The species can be found in forests in the north and east of Argentina. Under culture the stems sprout in June, produce flowers during October and dry down in January. During the rest period watering should not be suppressed. Watering during August and September is crucial for the development of flowers. In dry winters many of the plants do not bloom at all. Zone 9 A; Index V (Fig. 5)



Figs 1-16: ARGENTINE TERRESTRIAL ORCHIDS 1. *Habenaria gourleana* 2-3. *Habenaria hyeronimi* 4. *Habenaria parviflora* 5. *Chloraea membranacea* 6. *Chloraea magellanica* 7-8. *Sacoila lanceolata* (reddish flowers) 9-10. *Sacoila lanceolata* (yellowish flowers) 11-12. *Sacoila* sp. 13-14. *Skepsrostachys paraguayensis* 15-16. *Pelexia* sp.



Chloraea magellanica. Perennial herb from 30 to 60 cm tall, with fleshy roots with large, white and green veined, fragrant flowers, grouped in spikes. The species can be found in open areas, shrublands and grasslands near forests in the southwest of Argentina. Under culture the stems sprout in August, produce flowers during January and dry down in March. During the rest period watering should not be suppressed, but temperatures below 8°C for at least 60 days are required. Zone 7; Index I (Fig. 6).

Sacoila lanceolata (reddish flowers). Perennial herb from 50 to 80 cm tall, with fleshy roots. Flowers are reddish with a white labellum, grouped in spikes. Flowers are visited by hummingbirds (Galletto et al, 1997). The species can be found in dry shrublands and grasslands in central Argentina. Under culture the stems sprout in August, produce the flowers from September to November, and dry down in April. During the rest period (May to August) watering must be completely suppressed. Zone 9A, 9B; Index III (Figs. 7, 8).

Sacoila lanceolata (yellowish flowers). Plant is similar to the former but the flowers are yellowish with a white labellum, or the outer tepals are light yellow and the inner tepals are white. The populations that we found with this flower color came from the northeast of Argentina, growing in shrublands or forests. Under culture the leaves remain throughout the year or the rest period is short (1 month) during September. Flowers are produced from November to December. Watering must not be withheld at any time. Zone 9B, 10A; Index IV. (Figs. 9, 10)

Sacoila sp. Perennial herb from 70 to 100 cm tall, with fleshy roots. Flowers are reddish with a yellow labellum, grouped in condensed spikes. The species can be found in stony places in northwest Argentina. Under culture the stems sprout in October, produce flowers in February, and dry down in April. During the rest period (May to September) watering must be completely withheld. Zone 9 B; Index I (Figs. 11, 12).

Skeptrostachys paraguayensis. Perennial herb from 25 to 40 cm tall, with fleshy roots. Flowers are white, grouped in condensed spikes. The species can be found in grasslands or savannas in northeast Argentina. Under culture, the leaves remain throughout the year. Flowers are produced from January to March. Water need not be withheld. Zone 9B; Index V. (Figs. 13, 14).

Pelexia sp. Perennial herb from 30 to 50 cm tall, with fleshy roots. Flowers are white, grouped in condensed spikes. The species can be found in stony grasslands in central Argentina. Under culture the stems sprout in October, produce flowers during February and March, and dry down in April. During the rest period (May to September) water must be completely withheld. Zone 9B; Index III (Figs. 15, 16).

CONCLUSIONS

The species studied come from different kind of climates and soils, most of them growing in wet to dry grasslands. Under culture they bloom normally and, if hand pollinated, produce seeds. Our observations suggest that the success in cultivating the species with hardiness index I to III lies in making sure that no water is received during the rest period.

Recently some species of terrestrial orchids has been introduced as new ornamental crops, e. g. *Chloraea* in Chile (INDAP, 2001). Some of the species studied have potential as ornamental crops. *Chloraea membranacea* and *Skeptrostachys paraguayensis*, for example, can be easily cultivated in Buenos Aires, grown in shaded humid places in the garden.

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Table 1. Geographical distribution, location, habitat and soil features of the studied species.

Species	Geographical Distr. in Argentina	Location of the cultivated individuals	Habitat	Soil
<i>Habenaria gourleana</i>	North and Central	Buenos Aires Province, vicinities of Mar del Tuvu	Wet areas between dunes	Sandy wet soils
<i>Habenaria hyeronimi</i>	Central	Cordoba, El Zapato	Rocky hills	Sandy soils between rocks
<i>Habenaria parysiflora</i>	North east	Corrientes, Garruchos	Grasslands	Humid soils
<i>Sacola lanceolata</i> red flowers ¹	Central	San Luis, Papagayos Cordoba, El Zapato	Dry grasslands	Sandy soils
<i>Sacola lanceolata</i> yellow flowers ¹	North east	Corrientes, Santiago del Estero	Grasslands	Sandy soils
<i>Sacola</i> sp.	North west	Salta, Escoipe	Rocky Slopes	Sandy soils between rocks
<i>Chloraea membranacea</i>	Central	Buenos Aires, Magdalena	Dry forest	Calcareous soils
<i>Chloraea magellanica</i>	South	Rio Negro, Bariloche		Sandy soils between rocks
<i>Skeptrostachys</i> <i>paraguayensis</i>	Central	Entre Rios, Colon	Grasslands and savannahs	Sandy soils
<i>Pelexia</i> sp.	Central	Cordoba, El Zapato	Rocky hills	Sandy soils between rocks

POLLINATION AND PLOIDY CHANGES IN SOUTH AUSTRALIAN
POPULATIONS OF BULBIL WATSONIA, *WATSONIA MERIANA* (L.)
MILLER VAR. *BULBILLIFERA* (J. MATHEWS & L. BOLUS) D. A.
COOKE (IRIDACEAE)¹

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ABSTRACT

Watsonia meriana (L.) Miller var. *bulbillifera* (J. Mathews & L. Bolus) D.A. Cooke (Iridaceae) is a viviparous, geophytic weed which is naturalised across much of temperate southern Australia. However, despite being a sterile triploid, plants were noted from a number of localities in the Adelaide Hills, South Australia that were setting low levels of viable seed. Field observations suggest that there has also been successful adaptation by local pollinators to utilise this South African invader, with Meliphagid honeyeaters replacing the Nectariniid sunbirds which visit these flowers in southern Africa, although honeybees were also important potential pollinators. Cytological investigation revealed that, despite most of the parental corms being triploid, the seedlings derived from these seeds were diploid. The low levels of seed set and fertile pollen observed probably represent high failure rates at meiosis, with very few functional gametes produced by the triploid parents. The apparent ability of the plants to revert from triploids to bulbilliferous diploids that are morphologically similar to their triploid progenitors supports Cooke's argument for separate varietal status for the taxon.

¹ This paper was peer-reviewed prior to publication.



Fig. 1. *WATSONIA MERIANA* VAR. *BULBILIFERA* GROWING ON ROADSIDE VERGES IN THE ADELAIDE HILLS, SOUTH AUSTRALIA. **A.** Flowering plants showing the dense monoculture-like colony structure. **B.** Close up of flowers. **C.** Late season colony showing extensive aerial cormel development. **D.** Close up of cormels exhibiting precocious sprouting.

INTRODUCTION

The introduction of exotic and ornamental plants to South Australia over the past 166 years has resulted in numerous South African garden escapes finding the climate and ecological conditions of the state ideal in which to establish in both natural vegetation and agricultural systems (Kloot, 1987a, b, c). In particular, *Watsonia meriana* (L.) Miller var. *bulbillifera* (J. Mathews & L. Bolus) D. A. Cooke is a weed in Australia, Mauritius, Réunion and New Zealand (Goldblatt, 1989; Parsons and Cuthbertson, 1992) and has invaded the foothills and pasture lands of the state's southern areas. It is a declared noxious weed within most southern Australian states (Animal and Plant Control Commission, 1986; Carr et al., 1992; Lazarides et al., 1997).

Watsonia meriana var. *bulbillifera* (Figs 1A–B) is a cormous perennial native to Southern Africa, and is known variously as bulbil watsonia, bugle lily, wild watsonia (Cooke, 1986) and Merian's bugle lily (Parsons and Cuthbertson, 1992). *Watsonia meriana* belongs to the Lilianae: Iridaceae, is a member of the tribe Watsonieae (Goldblatt, 1998), and its synonyms include *Antholyza meriana* L., *Gladiolus merianus* (L.) Thunb., *Gladiolus amoenus* Salisb., *W. leipoldtii* L. Bolus, *W. vivipara* J. Mathews & L. Bolus, and *W. bulbillifera* J. Mathews & L. Bolus (Roux, 1980; Goldblatt, 1989). Goldblatt (1989) reduced the viviparous *W. bulbillifera* to *W. meriana* 'Bulbillifera' (J. Mathews & L. Bolus) Goldblatt, noting that the ability to grow reproductive propagules (bulbils or cormels) had evolved several times. *W. meriana* var. *meriana* often produces cormels within the axils of the lower leaves and branch axils (= *W. vivipara*), although not to the extent of var. *bulbillifera*, which produces them at all nodes along the flower spike (Figs 1C–D). He described its natural distribution as the Cape winter rainfall area of Southern Africa, where it typically grows in sand or thin rocky soils, and *W. meriana* 'Bulbillifera' was thought to be a sterile triploid sport which arose in, or has been introduced, into cultivation. Nevertheless, because it differs consistently from the type form in a number of features, Cooke (1998a) subsequently raised the taxon from cultivar to varietal status.

Within South Australia there are several naturalised *Watsonia* spp. (Jessop and Toelken, 1986), as well as a number of wild-growing named cultivars of probable hybrid origin (Cooke, 1998b). The earliest record of *W. meriana* var. *bulbillifera* in South Australia dates from 1842 at Camden Park, Adelaide (Parsons and Cuthbertson, 1992). Within the state it tends to infest pastures and nature reserves, occurring mainly from Victor Harbour to the

Barossa Valley, and in the south east corner of the state (Jessop and Toelker¹ 1986; Dashorst and Jessop, 1990). Infestation is most evident along roadsides, where it invades remnant natural vegetation. The resulting stands are generally impenetrable for other plants, and agricultural land can also be made redundant (Lamont, 1993; Wilson, 1993; Wilson and Conran, 1993), in contrast to Goldblatt's (1989) observation that *W. meriana* 'Bulbillifera' did not invade undisturbed native vegetation or arable land.

Although specimens of non-bulbilliferous *W. meriana* var. *meriana* were observed at Gumeracha and Echunga, growing amongst stands of var. *bulbillifera*, they were uncommon. Similarly, non-bulbilliferous plants assigned to *W. meriana* and *W. leipoldtii* (narrow-flowered forms) have been reported from Western Australia, also growing with bulbilliferous forms (Howard, 1993; Mueller, 1993).

Watsonia meriana var. *bulbillifera* sprouts in mid-Autumn after sufficient rain, flowering from October to Mid December, with aestivation (die-back) by late January. The shoot grows to a height of 60–70cm, bearing four to seven sword-shaped leaves that enclose the inflorescence. The scape reaches ca. 2 m, and bears 6–12 bright orange, curved, tubular flowers (Fig. 1B), with lower flowers on the scape replaced by cormel clusters.

The distinguishing characteristic of var. *bulbillifera* is the formation of vegetative reproductive propagules at the nodes of the flower stalk, referred to variously as cormels (Parsons and Cuthbertson, 1992; Cooke, 1998a), bulbils (Cooke, 1986), or cormlets (Goldblatt, 1989). Cormels are miniature corms with short curved beaks, and are asexual propagules. They form prior to anthesis in the axils of each node from the base of the plant to mid-way through the inflorescence. The bracts that encase them split open just prior to flowering. The cormels are dispersed at die-back in summer and stay dormant until the next winter wet season, or they remain attached and begin to grow *in situ* on old inflorescences (Fig. 1D). They develop in much the same way as the adult corm, but plants developing from cormels do not flower until the second or third year (Parsons and Cuthbertson, 1992).

Watsonia meriana var. *bulbillifera* is considered to be a sterile triploid (Goldblatt, 1971, 1989; Goldblatt and Takei, 1997), and thus should not normally set seed. Nevertheless, Mathews and Bolus (1922) observed partially fertile plants at the type locality of *W. bulbillifera* and Cooke (1998a), based on field observations and data from Wilson (1993), suggested that there may be apomixis and/or chromosomal ploidy alterations leading to seed production.

As a result, our study examined the hypothesis that seed set in the sub-fertile Adelaide Hills populations of *W. meriana* var. *bulbillifera* is the result of changes in ploidy. As part of this, pollination studies were also undertaken with the cytological investigations to determine whether pollinator availability might be involved as a potentially limiting factor.

MATERIALS AND METHODS

Five sites located in the Adelaide Hills were selected where plants were observed that were morphologically identical to var. *bulbillifera*, but which bore capsules as well as cormels. At each locality a number of features relating to pollination strategy, potential pollinators (visitors) and fecundity were recorded for all flowering plants (capsule bearing plants were not able to be distinguished at flowering), and seeds and cormels were collected from capsule-bearing plants for cytological study. Vouchers and living collections are held at the ADU and/or AD herbaria.

SPECIMENS EXAMINED

South Australia: 2 km WNW of Balhannah on Greenhill Road, 34°59'S 138°43'E, 17 Nov. 1993, J. G. Conran 687 (ADU); c.1.5 km ENE of Mylor along Hawthorn Road, 35°02'S 138°46'E, 17 Nov. 1993, J. G. Conran 687A (ADU); 7 km N of Gumeracha along road to Kersbrook, 34°47'S 138°53'E, Sept 1993, J. G. Conran 687B (ADU); 2 km NE of Kersbrook along road to Williamstown, 34°46'S 138°47'E, 2 Nov. 1996, J. G. Conran 778A (ADU); S side of freeway 1.2 km NW of Hahndorf entry, 7 Nov. 1996, D. A. Cooke 726 (AD, ADU)

REPRODUCTIVE BIOLOGY

Nectar. *Watsonia* flowers from ten plants were collected from each site, nectar was removed from the flowers using micropipettes, and nectar concentration (as sucrose equivalent) was determined for each plant by use of a Abbe refractometer (Dafni, 1992). In addition, a pooled nectar sample for each site was subjected to paper chromatography using an aqueous solution of n-butanol and acetic acid. After 24 hours, the paper was removed from the solvent, dried, stained in an indicator solution of aniline, diphenylamine and phosphoric acid and baked at 85°C for 5 minutes, following the method of Neimietz and Hawker (1988).

Pollen. Buds within two days of anthesis were collected into 70 ethanol. Three anthers per flower were opened under a dissecting microscope and the

number of pollen grains counted on a grid-lined slide. In addition, fresh pollen was removed from open flowers and stained in a 15% sucrose:10% methylene blue solution by the 'hanging drop' method for 24 hours to determine pollen germination and stainability as a guide to fertility (Dafni, 1992).

Ovules and seeds. Ovaries were removed from the flowers and the ovules counted. At the end of the season, capsules were collected and the number of seeds recorded. The ratios of pollen grains to ovules and seeds to ovules were then calculated, as well as the proportion of plants that produced capsules, the number of capsules per inflorescence and of seeds per capsule.

Viability and germination. Because of the low relative numbers produced, five seeds from each population were assessed for viability using the tetrazolium test (Cottrell, 1948). The remaining seeds were soaked for 72 hours in a 100 ppm Gibberellic Acid (GA_3) solution, planted out in pots of moist, 1:1 peat and sterilized coarse river sand and incubated under natural lighting in an unheated glasshouse for up to 12 months. Germination was recorded. Cormlets removed from the parental plants, and some parental corms were also placed into cultivation under the same conditions.

Pollinators. Visitors to flowering *Watsonia* at each site were recorded over the flowering period, with observations at each site lasting several hours between 8 AM and 4 PM, with the order and times of the site visits randomised to allow for varied pollinator activity. The species and behavior of any birds seen visiting was noted, and insect visitors were captured for later identification.

CHROMOSOMES

Root tips from the seedlings, resprouting corms and cormlets were harvested at several weeks of age and pretreated for mitotic arrest with 2 mM 8-hydroxyquinoline for four hours at 20°C. The treated root tips were fixed in 3:1 ethanol:glacial acetic acid for 24 hours at 0°C, washed and stored in 70% ethanol at -20°C. They were then washed in distilled water (5 mins), hydrolysed in 1 M HCl for 10 mins at 60°C, rewashed in distilled water (5 mins) and stained with Feulgen's solution for 1 hour. Following washing in tap water (10 mins) and then distilled water (5 mins), the meristems were macerated onto a slide in a drop of 45% acetic acid and squashed. Coverslips were removed by freezing in liquid nitrogen and the squashes air-dried overnight. Counter-staining used 4% Giemsa stain buffered in a 1:1 mixture of 1 M NaH_2PO_4 and 1 M Na_2HPO_4 (10 mins), before rinsing in distilled water, air-drying and mounting in Gurr's DPX[®].

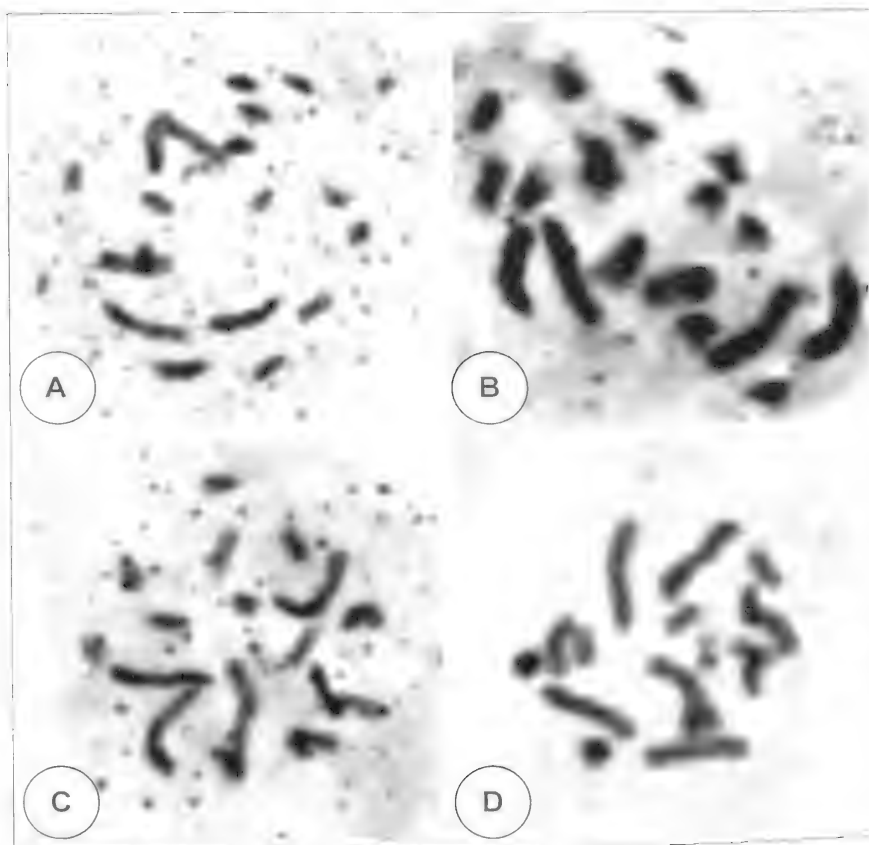


Fig. 2. CHROMOSOMES OF DIPLOID *WATSONIA MERIANA* VAR. *BULBILLIFERA* **A–C.** Seedlings ($2n=18$) of triploid, bulbiliferous parental plants from different populations from the Adelaide Hills, South Australia. **A.** Balhannah Conran 687 (ADU). **B.** Mylor Conran 687A (ADU). **C.** Kersbrook Conran 778A (ADU). **D.** Diploid mature plant from Hahndorf Cooke 726. (ADU). Scale bars = 1 μ m.

Chromosome measurements and counts were obtained from photographs of the best five metaphase plates for 2–3 individuals (where possible) of each population of each species.

RESULTS

Reproductive biology. The flowers of *W. meriana* var. *bulbillifera* are unscented and classed as part of the long-tubed, red-flowered species group within the genus that are thought to be sunbird-pollinated (Goldblatt, 1989). Nectar volumes were reasonably high at all sites, with sugar concentrations averaging around 20%. Subjective assessment of relative composition based

on chromatogram spot intensity (Percival, 1961) suggested that the proportions of sucrose, fructose and glucose were balanced or with a slight predominance of hexose sugars.

Watsonia meriana var. *bulbillifera* produces 60–280 cormels plant⁻¹ season⁻¹, resulting in potentially c.16,500 cormels m⁻²season⁻¹ (Wilson, 1993). Within most of the populations examined (Mylor being the exception) capsule bearing plants were relatively common (14–71%), despite pollen at all sites except Hahndorf (at 30%) being apparently infertile (Table 1). The numbers of seed set at each site were very low, both relative to ovule number (0.14–0.31%) and per capsule (1.8–3.9). Nevertheless, all seeds set were apparently viable, based on the tetrazolium test, and showed reasonable germination rates (40–80%).

Approximately 10 species were seen visiting *Watsonia* flowers in the Adelaide Hills (Table 2). The birds included two common Honeyeaters (Meliphagidae), as well as occasional Superb Blue Wrens. The most commonly observed insects were honeybees (*Apis mellifera*), although 2 species of blowfly, a hoverfly, chironomid midges and two beetle species were also observed in the flowers.

Amongst these visitors, the only species which appeared to exhibit foraging behaviour were the honeyeaters and honeybee, all of which fed actively on the nectar, and in the case of the bees, also collected pollen. The hoverfly and cantharid beetle were also active in the flowers, but they were seen much less frequently.

Chromosomes. All seedlings examined were found to be diploid (Fig. 2), regardless of origin. In contrast, the seeds at all sites except Hahndorf were borne on parents having triploid parental corms, the Hahndorf plants being diploid (although morphologically identical to triploid var. *bulbillifera* plants both there and elsewhere). The karyotype consisted of 2 long and 7 short pairs of chromosomes, with one of the short pairs having a satellite on the distal short arm, agreeing with previous reports (Goldblatt, 1971, 1989; Goldblatt and Takei, 1997).

DISCUSSION

In order for successful seed set, the populations must not only produce fertile pollen and viable ovules, but there needs to be adaptation by local pollinators to fill the niche that would be occupied in South Africa by Nectariniid sunbirds (Goldblatt, 1989). The copious dilute nectar and scentless, tubular, bright orange flowers mean that the flowers are well-advertised

and conform to a typical bird-pollination syndrome (Faegri and van der Pijl, 1979). Visitor observations confirmed that the local Meliphagid honeyeaters had added *Watsonia* to their diet. In addition, the abundance of honeybees on the flowers mirrors the condition observed for orange-pink South African *Watsonia* flowers, where bees are considered to be opportunistic pollinators (Goldblatt, 1989).

The hoverflies and cantharid beetles seen in the flowers may also represent opportunistic pollinators (Faegri and van der Pijl, 1979), although both are also known to be pollen feeders (Colless and McAlpine, 1991; Lawrence and Britton, 1991). In contrast, the visits by Splendid Fairy Wrens more likely represent predation on insects in the flowers, as these birds are primarily insectivorous (Rowley, 1965).

Seed set in *Watsonia meriana* var. *bulbillifera* was unexpected given the predominance of triploid plants. That seeds were set on plants which were morphologically identical to var. *bulbillifera* (i.e. taller, more robust plants with few-branched scapes, numerous cormels and fewer flowers), and which were mostly cytologically triploid, suggests that the seedlings were the result of low rates of successful chromosome assortment at meiosis, producing fertile offspring. This suggests either that random aneuploidy has occurred through the removal of the superfluous chromosome set, or that the plants have some ability to auto-adjust, as is seen in some polyploid *Rosa* hybrids, where long-term vegetative propagation can lead to increased fertility and the "ignoring" of superfluous chromosomes at meiosis (Fagerlind, 1958). Similarly, the ability to go independently from diploid to triploid multiple times within a species has been observed in *Hydrilla* (Nakamura et al., 1999). The reverse seems to be true in *Watsonia*.

The presence of mature diploid "var. *bulbillifera*" plants at the Hahndorf site suggests that the population here has been established longer and that seeds have matured to produce fertile adults. This also helps explain the much higher pollen fertility levels at this site, as the randomly sampled plants there apparently represent a mixture of mature diploids and triploids. The low seed set at this site is then difficult to explain. On the other hand, seed set at the sites with low pollen fertility may represent transfer of fertile pollen from the occasional non-bulbilliferous var. *meriana* plants seen at these sites.

The mature diploid plants at Hahndorf are morphologically identical to var. *bulbillifera*, and do not seem to represent reversion to the diploid taxon described as *W. vivipara*, as it produces only a few cormels in the lower leaf

axils. Having studied a wide range of *W. meriana* populations, Goldblatt (1989) concluded that the ability to make axillary cormlets is widespread, has evolved several times in the species and is thus of limited taxonomic significance, especially since cormels are also occasionally encountered in other *Watsonia* species (Goldblatt, 1989; Cooke, 1998a). However, as Cooke (1998a) noted, var. *bulbillifera* differs consistently in a number of inflorescence and floral features, and the presence of diploid plants which are still morphologically identical to var. *bulbillifera* tends to support his recognition of the taxon at the rank of variety. The presence of sexually reproductive plants could also help to explain the range of morphological variation seen within this taxon in the Adelaide Hills.

Alteration between sexual and asexual strategies with changes in ploidy is similar to the condition reported in *Ornithogalum umbellatum* L. (Hyacinthaceae) in France, where diploids are primarily sexual and the $3n$ – $6n$ polyploids are mainly asexual (Moret, 1991). Similarly, the sexually reproductive *Ornithogalum* populations were primarily outcrossing (van Raamsdonk, 1985; Moret, 1991). This situation is apparently analogous to the case in *W. meriana* var. *bulbillifera* where most of the plants are triploid and have very low pollen fertility. External pollen is almost certainly required, helping to explain the very low levels of seed set, even in the diploid adults at the Hahndorf site.

In conclusion, *W. meriana* var. *bulbillifera* in the Adelaide Hills appears to represent an example of a sterile triploid which has produced, by aneuploidy, fertile diploid seedlings. These offspring appear to retain the parental characteristics which help to define var. *bulbillifera*, supporting its retention as a separate taxon.

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Table 1. Reproductive features of *W. meriana* var *butillifera* at five sites in the Adelaide Hills. Gum: Gumeracha; Bal: Balhanna; Myl: Mylor; Ker: Kersbrook; Hah: Hahndorf.

Feature	Gum	Bal	Myl	Ker	Hah
Nectar volume per flower (μL)	50-63	87-96	43-75	54-78	60-90
Nectar concentration (mean \pm SD)	19.4 \pm 5.0	18.7 \pm 4.8	20.3 \pm 5.6	21.2 \pm 4.3	19.2 \pm 4.6
Nectar composition*	SFG	SFG	SFG	SFG	SFG
Pollen grains per ovule	2,054	1,984	2,369	1,882	1,904
Pollen fertility (%)	0	0	0	0	30
Ovules per flower (mean \pm SD)	23.8 \pm 2.5	20.1 \pm 2.0	21.4 \pm 4.1	25.2 \pm 4.7	23.1 \pm 3.1
Plants with capsules (%)	66	66	0.01	71	14
Capsules per fruiting scape (mean \pm SD)	1.5 \pm 0.9	1.5 \pm 0.8	1.0 \pm 0.9	1.9 \pm 1.2	1.4 \pm 1.1
Seeds per ovule (mean \pm SD)	0.2 \pm 0.04	0.18 \pm 0.03	0.14 \pm 0.07	0.31 \pm 0.09	0.22 \pm 0.04
Seeds per capsule (mean \pm SD)	3.9 \pm 1.4	2.7 \pm 1.1	1.8 \pm 0.9	3.6 \pm 1.6	2.9 \pm 1.7
Percentage viable seeds	100	100	100	100	100
Percentage seed germinated	80	60	80	40	60

* S = sucrose; F = fructose; G = glucose; Bold versus normal = intense versus moderate spotting on the chromatogram; SFG indicates both balanced and abundant sugars (after Percival 1961)

Table 2. Visitors to flowers of *W. meriana* var. *bulbillifera* in the Adelaide Hills.

Class	Family	Taxon	Common Name
Aves	Maluridae	<i>Malurus cyaneus</i>	Superb Blue Wren
	Meliphagidae	<i>Manorina melanoccephala</i>	Noisy Miner
		<i>Phylidonyrs novaeollandiae</i>	New Holland Honeyeater
Insecta	Apidae	<i>Apis mellifera</i>	Honeybee
	Calliphoridae	<i>Crysoxa</i> sp.	Blowfly
		<i>Calliphora stygia</i>	Eastern Golden-Haired Blowfly
	Syrphidae	<i>Simosyrphus grandicornis</i>	Common Hover Fly
	Chironomidae	Genus and species indet.	Midges
	Coccinellidae	<i>Cassida foreitana</i>	Ladybird Beetle
	Cantharidae	<i>Chauliognathus lugubris</i>	Plague Soldier Beetle

A NEW *CRINUM* SPECIES (AMARYLLIDACEAE) FROM ZAMBIA

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In 1994, D. Hardy from the National Botanic Institute in Pretoria, N. Lehmler, and I set out upon a field expedition in Zambia, the primary purpose being to pursue a study of indigenous *Crinum*. We arrived in Lusaka on 18 December and immediately rented an automobile, which much to our surprise came equipped with a mandatory driver. Then with what meager information we could acquire about prevailing weather conditions, we plotted our agenda and set out the following morning upon a nine day journey.

We initially proceeded to the west on the road to Mongu, and soon we were greeted with multiple sightings of *C. macowanii* Baker in bloom and in seed, these bulbs generally found in localized areas prone to temporary flooding. Then near the East Gateto Kafue National Park, we found *C. rautanenianum* Schinz in bloom within several small streams that traversed the highway. Later in the afternoon, we saw many *C. verdoorniae* Lehmler blooming along the banks of a river 43 km east of Kaoma. At 11 km east of Kaoma, *C. rautanenianum* was growing in the bed of a small dry stream while *C. verdoorniae* dotted the shoreline. As dusk was approaching, we observed rare bulbs growing in sand within savannah forest, the identity of which was uncertain. These non-blooming mystery bulbs were large and displayed green, undulating ciliate leaves as wide as 12 cm.

The following morning we were disappointed in being unable to explore the flood plain of the Zambesi River since the roads were poor and a 4-wheel-drive vehicle was required. On the return trip, we elected to spend the night at the Chunga Safari Camp on the banks of the Kafue River, a short distance from the North Gate to Kafue National Park. The drive to the Camp from the North Gate proved to be exciting, because a large black cobra slithered across the road while we watched from our vehicle. After we arrived at the Camp, I explored the nearby river bank and soon discovered bulbs of *C. subcernuum* Baker growing about 5 m from the water's edge. That evening, our tranquility was frequently interrupted by hippopotamus calls from the nearby river. We were warned not to wander about the Camp after dark.

We spent much of the following day within the Kafue National Park where we observed many *C. macowanii*. We hiked through a very promising dolomite locality east of the Park, where we saw *Ammodramis coranica* (Ker-Gawl.) Herbert and a *Boophone* species, but not a single *Crinum* was to be found. We returned to Lusaka and spent the night at the Pamodzi Hotel.

The next day we commenced the long drive to Livingston. During the initial 150 km, we occasionally observed both *C. macowanii* and *C. rauatanenianum* in flower, always in riverine conditions. We came upon a cluster of the mystery *Crinum* northwest of Livingston; none were in flower, but there were old scapes of circa 10–12 flowers. Small numbers of compressed pithy seeds lay scattered about the bulb bases. During the last 20 km of our drive, we saw many bulbs of *C. crassicaule* Baker. These were growing in red sand, and although I inspected about 40 bulbs, only one had flowered and bore the characteristic dark papillose seeds.

Sadly Victoria Falls was not impressive. The Zambesi River water level was quite low at the time. We stayed two nights at the Musi-O-Tunya Hotel, and, during our stay, we visited the Musi-O-Tunya Game Park where we saw a large number of animals including rhinoceros. On the return trip to Lusaka, we encountered heavy rains. However, north of Monze we found another cluster of the mystery *Crinum* growing in red sand within a wooded savannah. This time one bulb was in fruit—small orangish globes on long pedicels. I was bewildered as to the identity.

The following day was Christmas, and we drove north to Kitwe. One local Christmas custom was peculiar to us; people celebrated the holiday with fire-crackers. There was also much partying on Christmas eve, and our departure was late because our driver suffered from a “hangover.” Between Kabve and Kapiri we saw many of the mystery *Crinum* in fruit, and this afforded the opportunity for a detailed study. Never though did we sight a bulb in bloom. During the drive we also observed several large copper mines.

That night we stayed at the Edinburgh Hotel. All of the hotel staff except the manager had been given the day off, and the only food available for dinner was left over wedding cake from the previous day.

We then attempted to drive northwest, but we encountered heavy rains and turned back after 160 km. There had been good rains in the region for weeks, and the grasses and brush were luxurious, making it almost impossible to sight *Crinum* from the highway. We did see the famous “slave tree” beneath which slaves were bought and sold long ago. We again spent the night at the Edinburgh Hotel.

Next morning we visited the Forest Department Herbarium at Kitwe. The Assistant Curator and her technician were most courteous and helpful. Sadly, there was little funding available to continue operating the Herbarium. There were a few *Crinum* specimens though, including an excellent dried mount of the mystery *Crinum* in fruit (Zambia. Ndola, 6



Fig. 1. Herbarium specimen of *Crinum aurantiacum* in fruit (Zambia: Ndola, 6 Dec 1960, JMM 89, NDO). Courtesy of the Forest Department Herbarium at Kitwe, Zambia.

Dec 1960, JMM 89, NDO. Fig. 1). We then departed for Lusaka, as the next morning we were scheduled to fly to Johannesburg.

CRINUM AURANTIACUM LEHMILLER, SP. NOV. (SUBGENUS *CODONOCRINUM*).

Species *C. forbesii* et *C. macowanii* interjecta, sed fructificatione aurantiaca differt.

Type: Zambia. Mwinilunga District, near River Kasompa. 8 October 1937, Milne-Redhead 2672 (Holotype, K).

Bulb globular, 12–15+ cm in diameter, tapering to an underground neck 7–9 cm long, covered with a thin tunic of light brown leaf scales; basal offsets not observed. Leaves 6–15, forming a rosette, arching to sprawling on the ground, all but new leaves concavely trun-

catated at the ends, broadly channeled and coarsely undulate, mild midline thickening but lacking a depressed midrib effect, margins prominently ciliate with cilia 2–4 mm long, bearing closely spaced longitudinal nerves with cross striations visible with a magnifying glass, containing minute wooly fibers when torn apart, green, 46–90+ cm long and 9.8–24.5 cm wide. Scape compressed, 8–27 cm long. Spathe with 2 principal external bracts, 11.5–13.5 cm long, reflexed and papery at anthesis, with multiple internal filamentous bracts. Umbel 10–21; flowers zygomorphic, pedicellate with pedicels 3.5–6.0 cm long, opening at night, weakly scented. Buds slender and very pointed, striped dark rust red, initially closely spaced and vertical, then elongating and slowly spreading apart through motion at the pedicle node; buds not inclining or drooping prior to anthesis. Perianth tube straight at anthesis, suberect, dull reddish green, 9.5–12 cm long. Segments lanceolate and slender, white with a pinkish-red dorsal keel, unequal with the outer segments longer and narrower, 9.1–12.3 cm long and 1.4–2.1 cm wide, apiculate, the outer segments bearing projections 6–7 mm long. Filaments 6, clustered together and bowed, white, unequal



Fig. 2. *Crinum aurantiacum* in flower. Bulb grown from seed collected at 57 km northwest of Livingston, Zambia, 22 Dec 1994.

with those attached to the inner segments longer, 6.6–7.6 cm long; anthers gray, pollen cream colored. Style pink distally and white proximally, 10.5 cm long; stigma weakly capitate. Fruit spherical, orange, with a sturdy fleshy pericarp 4–6 mm thick, 1.2–3.2 cm in diameter; seeds 1–13 per fruit, pithy and lacking a smooth seed coat, angulated and tightly compressed into parts of a sphere by the pericarp, germinating into the decaying walls of the pericarp.

Habitat: Wooded savannah, growing in sandy soil.

DISCUSSION

Herbarium specimen interpretation of *Crinum* is fraught with error. There are few species which possess unique features that are readily identified in herbaria. In addition, rarely do herbaria include fruit and seed which are important differentiating characters, and herbaria can never document the budding movements which Herbert (1821) thought to be of such importance that he included it in his subgeneric classification scheme. Accurate classification requires detailed observations of living plants during the complete flowering and fruiting sequence, as well as leaf configuration including margins and venation, bulb morphology, and habitat. Visits to holotype sites are sometimes necessary. Only then should attempts be made to correlate/study herbarium specimens. Soon, DNA sequencing may play a vital role, especially in disputed identifications.



Fig. 3. *Crinum aurantiacum* in fruit, 62 km southwest of Ndola, Zambia, 25 Dec 1994.

The important characters which *C. aurantiacum* possesses include: broad undulate leaves that are prominently ciliate, flowers with slender lanceolate segments and long pedicels (Fig. 2), orange fruit (Fig. 3) with a firm thick pericarp that lacks a rostellum, and non papillose seeds that lack a smooth surface. Two characters of importance are only appreciated in living specimens. First, the orange fruit forms a small compact globe that tightly envelopes the seeds, compressing them into parts of a single central sphere. The pericarp is very sturdy and measures 4–6 mm in thickness. During dehiscence, the pithy seeds germinate into the decaying pericarp. Secondly, when the spathe valves split apart, the buds begin to gradually separate from one another as they approach anthesis. This separation is accomplished by limited radial dispersion at the pedicel node; the perianth tubes remain completely straight until after anthesis. The buds do not move through any inclining or drooping motions prior to anthesis, a very unusual feature for subgenus *Codonocrinum*¹. Herbert would have been perplexed by *C. aurantiacum*.

When I first observed *C. aurantiacum* in the field, I considered the possibility that it was a giant variety of *C. macowanii* Baker because of the large undulate leaves. When I first observed its fruit, visions of *C. forbesii* (Lind.) Schultes emend. Herbert passed through my mind. After more field study, I

¹ Editor's note: DNA sequences indicate very strongly that the subgenera of *Crinum* are not natural groups. See Meerow, Lehmiller and Clayton, 2003. Bot. J. Linn. Soc. 141: 349–363.

became convinced it was neither of these two species. Unfortunately, it required seven more years before I was able to observe a cultivated bulb in bloom. Major character differences noted in *C. macowanii* include: fruit with a thin pericarp and possessing a rostellum, scabrous leaf margins, and inclining budding motion with a curved perianth tube at anthesis. Lesser characters include: broader segments, usually longer scapes, and usually shorter pedicels. Major character differences of *C. forbesii* include: red fruit with a thick but flexible pericarp that does not compress the seeds, ovoid seeds with a smooth shiny coat, non undulate leaves, and inclining budding motion with a curved perianth tube at anthesis. Lesser characters include: broader highly colored segments and sometimes larger umbels with 26–40 flowers. Both *C. crassicaule* Baker and *C. harmsii* Baker are readily separated on the basis of shorter pedicels, inclining bud motion, fruit bearing a rostellum, and papillose seeds.

Crinum pedicellatum Pax is a poorly defined species. Nordal (1977) considered it to be synonymous with *C. macowanii*, and I agreed with her (Lehmiller, 1997). Other than repetitions of the original account, the only other published record of *C. pedicellatum* familiar to me is the painting and brief description by Moriarty (1975); her painting is not *in-situ* and resembles *C. macowanii* – the pedicels are short, while the accompanying herbarium specimen (Malawi, Southern Region, 1970–74, A. Moriarty 712, K) is surely *C. macowanii*.

To distinguish *C. aurantiacum* from other Zambian species in herbaria is problematic. Rarely are fruit and seeds included in herbaria, and this makes the specimen at Kitwe (Zambia. Ndola, 6 Dec 1960, JMM 89, NDO) unique because it does include fruit. A specimen accompanied by a field photo, such as the holotype (Zambia. Mwinilunga District, near River Kasompa, 8 Oct 1937, Milne-Redhead 2672, K), may provide the necessary clues for proper identification. Otherwise, only an excellent quality specimen with clear detail of the flowering scape and leaves (Zambia. Abercorn District, 2 miles from Abercorn – now Mbala, 1 Dec 1958, Mrs. H. M. Richards 10783, K) can be used to differentiate *C. aurantiacum* from the multitude of other species of subgenus *Codonocrinum* occurring in Southern Africa.

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THE AUTECOLOGY OF *ZANTEDESCHIA JUCUNDA* AND
ZANTEDESCHIA PENTLANDII FROM SOUTH AFRICA'S
LIMPOPO AND MPUMALANGA PROVINCES

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Zantedeschia jucunda is endemic to the Leolo Mountains in Sekhukhuneland. The Leolo Mountains run in a north-south direction roughly through the center of Sekhukhuneland in Limpopo Province. *Z. jucunda* is found on the summit of the mountain range, mainly at an altitude of 1400–1800 meters. *Z. pentlandii* is found mostly in the Roosenekal and Tonteldoos areas of Mpumalanga. Most populations of these plants occur in hilly and mountainous areas, mainly at altitudes of 1600–1900 meters.

Both arum species have rich golden yellow flowers. This feature is relatively constant in *Z. pentlandii*, but varies a good deal in *Z. jucunda*. The spathes of *Z. jucunda* vary from rich cream through lemon yellow to dark yellow. The leaves of *Z. jucunda* are hastate and always copiously marked with white or cream spots. Some leaves also have raised ivory colored tubercles. *Z. pentlandii* usually has plain leaves, but in some populations plants with copiously spotted leaves are also found. The main externally visible factor distinguishing the two species is the consistently spotted hastate leaves of *Z. jucunda*.

Zantedeschia jucunda was described by Cythna Letty (1961). Readers are referred to the formal description (Letty, 1961) and also to her revision of *Zantedeschia* (Letty, 1973) in which further details are given as to the taxonomy of this species. The reasons given by Letty for upholding *Z. jucunda* as a species may be amplified by future workers using some of the tools of modern taxonomy. It is also quite possible that *Z. jucunda* could be a variant of *Z. pentlandii*, and perhaps future workers will take this view. At the autecological level there is only one major difference that could be found between the habitat niches occupied by the two species. Overall, there is much similarity.

It would be interesting to determine if yellow-flowered arums are found on the Thaba Sekhukhune immediately south of the Leolo Mountains, the Dwars River Mountains to the south east, and the Schurinksberg and its foothills, to the east. This area has not been thoroughly explored by botanists and if yellow arums are found, these populations might form connecting links with *Z. pentlandii* populations in the Roosenekal area.

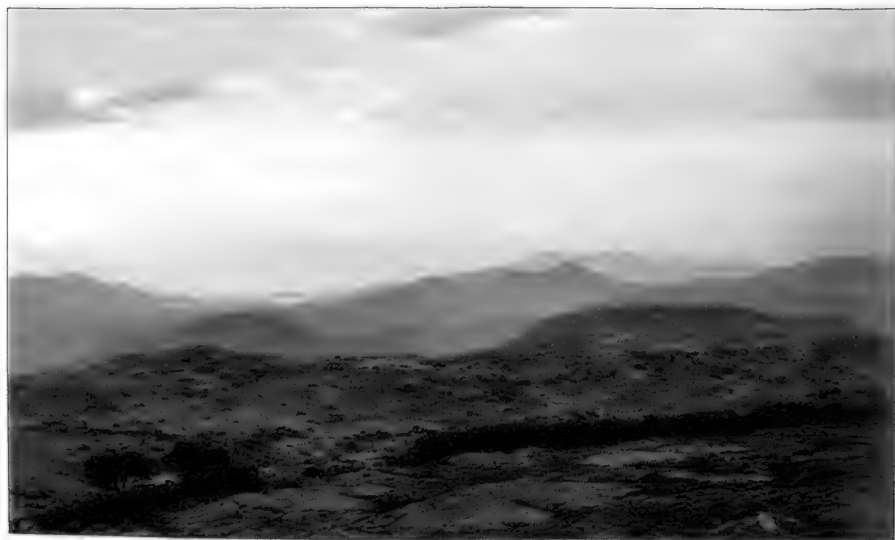


Fig. 1. The rocky summit of the Leolo Mountains the habitat of *Zantedeschia jucunda*. A thunderstorm is approaching in the distance. Summer thunderstorms are the typical precipitation received on the mountains.

There is an interesting and most informative chapter on the Sekhukhuneland Center of Floristic Endemism in the recent book by van Wyk and Smith (2001, pp.126–133). Readers are referred to this chapter for an account of the plant geography of Sekhukhuneland, the region in which the two yellow arums are found.

THE TWO STUDY AREAS

Zantedeschia jucunda was studied on the southern section of the Leolo Mountains, mostly at altitudes of 1600–1900 meters. *Z. pentlandii* was studied in the Chieftain's Plain area north east of Roossenekal at an altitude ranging from 1800–1900 meters. The most southerly part of the study area is in the hills and mountains south west of Tonteldoos, also at an altitude of 1800–1900 meters.

In the areas where both yellow arums occur, they live alongside the agricultural and pastoral pursuits of man. The southern sections of the Leolo Mountains are home to the Pedi people. They live in dense settlements below the mountains, and in smaller villages and scattered homesteads on the summit plateau. The niches occupied by *Z. jucunda* on the southern section of the Leolos are usually close to human settlement, and animals graze daily around many of the arum populations.

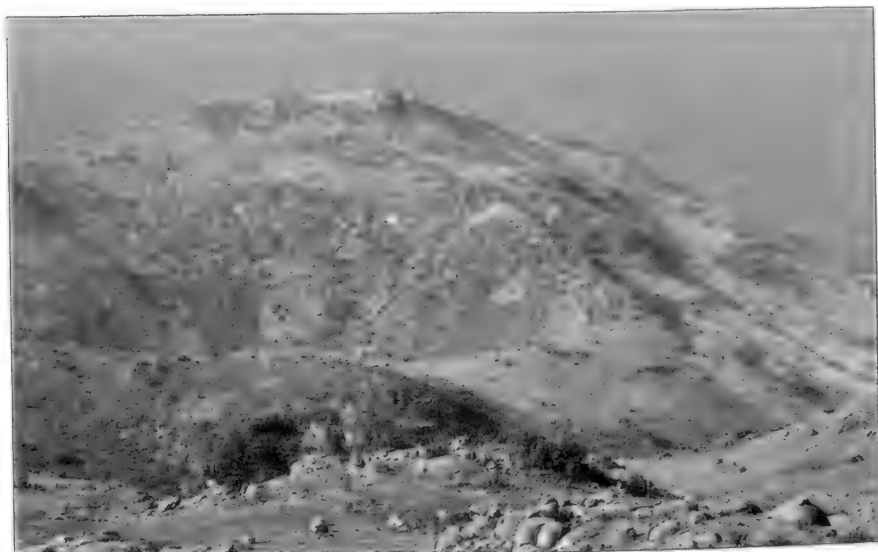


Fig. 2. Extensive stone walling high up on the summit of the Leolo Mountains. These walls comprise a significant part of *Zantedeschia jucunda* habitat on the mountain.

Zantedeschia pentlandii habitat is also close to human settlement. The main difference is that the region has been transformed to a greater degree than the equivalent habitat on the Leolo Mountains. The low-lying areas have largely been put under the plow. Consequently, *Z. pentlandii* is rare along streams in open grassland and in loam patches around rock outcrops. In addition, the area has seen a great increase in the number of porcupines in recent decades, which excavate and eat the bulbs. These matters are discussed in more detail below.

***ZANTEDESCHIA JUCUNDA* IN ITS MOUNTAIN TOP HABITAT**

All plants in the summer rainfall eastern portions of South Africa have evolved with fire and grazing. Prior to human settlement on the Leolos, fires were mostly caused by lightning strikes, and the mountain tops were grazed by various antelope. The summit of the Leolos are in a high lightning strike area, associated with their elevation above an extensive plain and the magnetic qualities of the rocks. In the modern environment the terrain is grazed all year round by cattle, goats and sheep. Fires are ignited either deliberately by the local people, often to stimulate the growth of new grass, or else as the result of fires that burn up the mountain from the lower, more densely inhabited areas. The flammable areas are burnt every year, but burns are not always



Fig. 3. *Zantedeschia jucunda* is frequently encountered growing in fissures on boulder cliffs on the Leolo Mountains. Plants with rich golden yellow spathes were those from which Cythia Letty drew up the type description of the species.

thorough, particularly in rocky areas which may serve as fire islands for some years. When the grass grows densely enough, these sites will burn once again. Crevices on boulder cliffs and fissures on sheets of exposed rock rarely carry much grass cover and are generally untouched by fires unless the area has not been burnt for several years.

Zantedeschia jucunda requires sites free from the clutter of moribund vegetation to grow and flower regularly. Fire and grazing by domestic stock plays a significant part in keeping the populations of these plants healthy. The arum leaves are not grazed, thus the only damage by livestock is the trampling of some plants that are not growing in rocky habitat.

Zantedeschia jucunda occupies the following distinct natural habitats: open loamy patches of soil, crevices in sheets of exposed rock, pockets of soil on boulder outcrops and fissures in boulder cliffs. A significant number of plants also occur in stone walls, built on various parts of the mountain summit by the local people. Plants are also found in stone graveyard walls, the stone walls of some homesteads, and piles of boulders in agricultural land. These man-made habitats serve the purpose of significantly extending the natural habitat available to the plants. Some of the larger groups of arums are currently growing in these situations. In places where walls are built over loamy areas, arums are readily able to germinate and take root. The heavy soil on the summit of the Leolo Mountains retains water well after rain. Large rocks and rock sheets funnel water over groups of arums, even after light showers of rain.

Zantedeschia jucunda flowers from late November until late December. Rainfall is not required to stimulate the largest bulbs to flower, and some

plants may be seen in flower in late November before rains begin. The first substantial rains of the season begin in December coinciding with the peak flowering season.

Zantedeschia jucunda flowers are pollinated by flying beetles which gather inside the spathes in large numbers, apparently to feed on the pollen. Flowers in groups in bright sunlight appear to attract the largest number of beetles. Pollination within groups of plants is very variable from one season to the next. It is for this reason that seedlings around the adult plants occur in batches of the same size. These varying age grades of the young plants can be used to ascertain which groups of adult plants in particular habitat niches are most successfully pollinated.

FACTORS AFFECTING *ZANTEDESCHIA JUCUNDA* POPULATION DYNAMICS

The presence of pollinators on specific parts of the mountain varies from one season to the next. There is currently no data available, collected over a period of several years, concerning the extent to which *Z. jucunda* populations are successfully pollinated.



Fig. 4. *Zantedeschia jucunda* often has creamy yellow flowers. The bulbs are frequently crowded together in rocky niches.

Plants are dug up during the vegetative and reproductive seasons by the local people. These are apparently sold to the horticultural trade. The plants are dug out in areas where they can be most easily removed, usually where bulbs grow in wide rock fissures or loamy soil. Most removals take place in areas closest to villages, homesteads or fields. In the extreme southern part of the Leolo Mountains, *Z. jucunda* is now scarce in places close to fields and settlements.

In many instances arums resprout from crevices where they have been removed, as some bulbs get damaged and are left behind, or smaller ones get the chance to grow. Only the large



Fig. 5. Some *Zantedeschia jucunda* populations have cream spathes with a rich burgundy wash.

flowering sized bulbs are currently attractive to gatherers. There is a huge reserve of young bulbs in some crevices where the larger ones are removed. The effect of these excavations is currently ideal for promoting the growth of young plants. It is noteworthy that bulbs are not removed everywhere on the mountain. The number of bulbs harvested also varies from one year to the next. In the 2002–2003 growing season many accessible bulbs were removed, but only a handful in the 2003–2004 season. There was an indication in the 2002–2003 and 2003–2004 growing periods that plants were not collected from stone walls, sites in fields, graveyard walls or homestead walls.

The long-term effects of harvesting large flowering bulbs from the mountain, year after year, will be to reduce the seed bearing capacity of some arum populations.

No indications of animal predation on the bulbs were found, and porcupines were not a problem (these animals are having a significant long-term effect on *Z. pentlandii* populations, discussed below).

The effects of global warming predicted for South Africa may have the effect of shrinking populations of this species to the rockiest habitats where bulbs are irrigated even after very light rain showers. There would also be probable changes to the arum populations if the grassland habitat on the summit of the Leolos were to be invaded by xerophytic scrub.

ZANTEDESCHIA PENTLANDII IN ITS MODERN HABITAT NEAR ROOSSENEKAL AND TONTELDOOS

Zantedeschia pentlandii once occupied a wider range of habitats than it does at present. The plants used to occur in open loamy areas near rocks and

beside streams. A photograph of groups of arums in such habitat can be seen in Letty's (1973) revision of *Zantedeschia* (p.16). The species is currently found mainly in rocky hilly areas, where it grows among boulders on rocky outcrops. The plants studied were in two areas separated by about 30 km.

The Chieftain's Plain study area. The Chieftain's Plain study consists of large boulder hills in the lower region and a tall extensive mountain in the higher region. The area is settled by local people who live in scattered homesteads on the plain. Stone walls are found around homesteads and graveyards and also on various parts of the mountain. The settlement pattern is identical to that on the southern section of the Leolo Mountains.

The distribution of *Z. pentlandii* in this area is the same as that on the summit of the Leolo Mountains. The plants grow in and beside stone walls, on boulder outcrops and in fissures on sheets of exposed rock. The arums were not observed growing on boulder cliffs, a regular habitat niche occupied by *Z. jucunda* on the Leolo Mountains. Boulder cliffs are just as common here as they are on the Leolo Mountains. Livestock is herded mostly on the grassy plains and the lower slopes of the mountains. Goats also graze on the rocky hillsides, but they do not currently occur in the same numbers as those kept on the Leolos. *Z. pentlandii* occupies all niches open to it in this area and may be quite common in open loamy areas, adjacent to rocky outcrops and dwellings.



Fig. 6. *Zantedeschia pentlandii* is most commonly encountered amongst rock outcrops. In these situations it is difficult for porcupines to excavate the bulbs.



Fig. 7. *Zantedeschia pentlandii* often grows near large sheets of exposed rock. In these situations the bulbs are well irrigated by runoff from even light rainstorms. The plants are frequently found growing with *Aloe castanea*, an identical situation to that commonly encountered on the Leolo Mountains.

No predation of bulbs by porcupines was noted near dwellings and vicinity. Seedlings of various ages were present near all groups of adult bulbs. In most cases they were at specific stages of development from batches of seeds that had germinated at the same time.

Research was conducted in January 2003 in order to ascertain how many flowers had been pollinated in various parts of the habitat. It was found that seed bearing plants were usually growing where several bulbs had flowered in the same or adjacent habitat niches. Pollinated flowers were mostly full of ripening seeds.

The population of *Z. pentlandii* is on the increase in this area with many young seedlings evident in various niches throughout the habitat. The country is kept clear of long and moribund grass by regular winter grass fires and year round grazing by domestic stock.

The Tonteldoos study area. The Tonteldoos study area differed from that at Chieftain's Plain in that most arable land had been put under the plough, and settlements were mostly farm homesteads dispersed over the area, predominantly on the plains or in valleys.

Zantedeschia pentlandii in this region is currently almost entirely restricted to rock outcrop habitats. There is virtually no increase in the numbers of plants as the rocky niches where the bulbs occur are fully occupied. Seeds do

sometimes germinate in washes besides sheets of exposed rock, but these are excavated and eaten by porcupines when they increase to a larger size.

In much of the habitat the rocky niches have too little soil for germination of *Z. pentlandii* seeds and development of the bulbs. Stone walls are not built by the farming community and consequently this extension to the natural habitat is unavailable. The equivalent of stone walls are lines of tumbled boulders beside secondary roads that have been dumped by earth moving machines during road maintenance and widening activities. These sites, although rare, are densely utilised by *Z. pentlandii* wherever available. The soil at the base of these boulder walls is ideal for the germination of *Z. pentlandii* seeds, and development of bulbs in sites that cannot be reached by porcupines.

Fire is the main agent responsible for keeping the habitat clear in the Tonteldoos study area. Burns on rocky hillsides are rather irregular, and in areas which escape burning for several seasons, few of the arums come into flower. Once the accumulations of moribund grass are burnt, these populations come into flower once again.

A study of pollinated *Z. pentlandii* flowers in January 2003 revealed the same pattern as the Chieftain's Plain study area. Flowers were pollinated close to one another where they grew in groups, but many plants that had flowered in the habitat had not been pollinated.

Beetles are also apparently the main pollinating agents of *Z. pentlandii* as is the case with *Z. jucunda* on the Leolo Mountains. Beetles are sometimes trapped in the base of the spathes where they are fully preserved until the spathe withers.



Fig. 8. Spotted leaved *Zantedeschia pentlandii* are quite often encountered. The color of the spathes is generally a rich golden yellow.

ZANTEDESCHIA PENTLANDII POPULATIONS IN AN ALTERED ENVIRONMENT

There has been an increase in numbers of porcupines associated with modern agricultural output (S. Siebert, personal communication) and a decrease in the number of porcupine predators, mainly jackals (Prof. A.E. van Wyk, personal communication). As a result, porcupines function to restrict *Z. pentlandii* populations to rocky niches where they cannot be excavated and eaten.

Porcupine predation is heavy at the beginning of the *Z. pentlandii* flowering season when these plants are very distinctive and visible. Once the main rains begin, there is a greater variety of bulbs for porcupines to eat and the pressures on *Z. pentlandii* are lessened. Many flowering bulbs get destroyed by porcupines early in the season, particularly if the rains are late in arriving. Flowers and leaves are often destroyed while porcupines try and remove bulbs from inaccessible rock crevices. Porcupines are likely to precipitate a decline in seed production in much of the hilly and mountainous habitat currently occupied by *Z. pentlandii*.

FURTHER READING

Additional information, on the yellow arums, is to be found in the following references:

- Craib C. *Zantedeschia jucunda* and *Zantedeschia pentlandii*, the beautiful yellow arums from the Sekhukhuneland Centre of Floristic Endemism. Veld and Flora September 2003: 106–109.
- Craib C. *Zantedeschia jucunda* populations on the Leolo Mountains in Sekhukhuneland (in ed.) Veld and Flora June 2004 (the editing should occur in April 2004 and if you would like to contact Caroline Voget, the editor of Veld and Flora for the full details, her email address is voget@kingsley.co.za).

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All photographs by Connall Oosterbroek.

**A NEW GENUS RELATED TO *TULBAGHIA* FROM
SEEPAGE AREAS ON THE SUMMIT OF THE LEOLO MOUNTAINS
IN SEKHUKHUNELAND, SOUTH AFRICA**

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Sekhukhuneland is a recognized center of floristic endemism (van Wyk and Smith, 2001). The region has a diverse flora rich in endemics, several of which remain to be formally described (Siebert et al., 2002). These endemic species are absent from other grassland and savanna areas of southern Africa, as they are adapted to the specific soil and climatic conditions of Sekhukhuneland.

Sekhukhuneland lies in the Limpopo and Mpumalanga Provinces of South Africa. It comprises large valleys with numerous concentric belts of undulating ultramafic hills. The Leolo Mountains run in a north-south direction through the centre of Sekhukhuneland, parallel and to the west of the northeastern Drakensberg Escarpment. Much of Sekhukhuneland is semi-arid and hot, lying as it does in the rain shadow of the Drakensberg. The Leolo Mountains, however, rise to over 1000 m above the dry valleys and subsequently receive the highest rainfall in the area. Rain falls mostly in the form of summer thundershowers, from December to April. Morning mist is quite common on the Leolo Mountains.

The Leolo Mountains are characterized by a summit plateau much of which lies higher than 1600 m above sea level. The summit plateau has heavy loam and clay soils derived from norite. Vast sheets of exposed norite are found on some of the elevated sections of the mountain. Seepage areas are found either at the base of these sheets of exposed rock or in depressions among boulder outcrops and their associated rock sheets. Some of the seepage areas are fed by small streams that run for most of the wetter summer months. The seepage areas are periodically very wet in summer and very dry during the rainless winter. During wet periods they are permanently saturated and the ground is sometimes covered by a few cm of water for months at a time.

The seepage areas differ from those in many other regions in South Africa in that the soil is black, with limited organic material. Because of the very high clay content, the soil drains extremely slowly. Small amounts of precipitation are enough to funnel substantial amounts of water off the rock



Fig. 1. The most extensive colonies of the new genus are found in seepage areas associated with vast sheets of exposed rock. In these situations the bulbs occupy every available niche. This habitat is rare and could very easily become degraded through increased human habitation in the Leolo Mountains.

sheets, saturating the seepage areas. This is, in fact, a very rare habitat, floristically much related to plant communities of seepage areas below the Drakensberg Escarpment at approximately 1800 m. Species typical of this seepage habitat on the Leolo Mountains include *Anagallis huttonii*, *Eucomis autumnalis* subsp. *clavata*, *Hypoxis filiformis*, *Limosella major*, *Ranunculus meyeri*, *R. multifidus* and *Sporobolus centrifugus*. It is furthermore characterized by the absence of trees and shrubs, with the mean height of the community hardly ever exceeding 30 cm.

This unusual niche also harbors a new genus that at present appears to contain only one species. The second author and Braam van Wyk of the University of Pretoria made the first collections of this species in December 1999. The plants appear to be closely related to *Tulbaghia*, and Clare and Robert Archer of the National Botanical Institute in Pretoria are currently working on the taxonomic placement of the genus. Recently, the *Limosella major*-*Ranunculus meyeri* High Altitude Seepages, in which the new genus occurs, was recognized, together with the *Brachiaria serrata*-*Melhanian randii* Rocky Grassland, as a conservation priority for the Sekhukhuneland Center of Plant Endemism. Whereas the Rocky Grassland is widespread in Sekhukhuneland (also on the plateau of the Leolo Mountains), the High Altitude Seepages are restricted to the plateau of the Leolo Mountains.



Fig. 2. The most common habitat where the new genus is found consists of seepage areas situated between large numbers of exposed boulders. Cow dung as seen in the center of this photograph enriches the soil, adding to the limited amount of organic material received from decomposed grass.

The bulbs of the undescribed species are very plentiful in the limited area of habitat that they occupy, and the plants are very conspicuous when in flower. It is interesting to note that when a plant starts to flower, it does so profusely, producing at least one open flower per day for approximately a week. This is usually followed by a resting phase and then a second spell of flowering (sometimes even a third). Flowers are readily pollinated, and seeds are produced during the wettest part of the summer when they stand the best chance of germination. The seepage areas with the highest concentration of bulbs are those kept permanently moist by streams. In these areas, bulbs number many thousands, closely packed together and ranging from flowering size to newly germinated. The only limiting factor to occupation of the specific niche by the plants is the density and large numbers of their own bulbs.

During prolonged periods of daily thundershowers, the streams flood and carry with them seeds and young bulbs that have not yet rooted deeply in the norite clay. Some seeds and bulbs may be washed into less suitable habitats. In such drier areas, the bulbs dry out and the seeds fail to germinate, while others land in suitable habitats where they can germinate and grow. Seeds or young bulbs are occasionally washed into grass tufts and moss beds beside the streams. Although such areas constitute marginal



Fig. 3. Some seeds of the new genus even manage to germinate and grow in thick moss beds where there is very little soil. Such sites are easily damaged by the hooves of grazing animals.

habitat, the bulbs can grow there as long as the spots are kept moist.

The southern section of the Leolo Mountains is inhabited by the Pedi, local indigenous people who farm stock and grow crops. Cattle and goats keep the grass cover on the mountain short. These animals also graze heavily around the seepage areas and keep them clear of moribund vegetation. They also fertilize the habitat with their droppings.

Cattle sometimes trample seepage areas as they move between grazing sites after heavy rainfall. The animals leave deep hoof prints in the clay, and thousands of bulbs are often displaced or squashed. Overall trampling of the seepage areas is rare since the rock sheet areas where they are found are largely unattractive to grazing animals.

The new genus has so far been found only on the southern section of the Leolo Mountains, but it may well occur in similar habitats all along the range. However, further north along the mountain range, the rainfall and the number of seepage areas decreases significantly. It seems as if the habitat of the species has now been isolated by a drier climate to the north and human activities to the south.

The extreme southern end of the mountains contains some seepage areas that have been degraded through siltation associated with prolonged settlement. These seepage areas dry out quickly after rain and are not occu-

pied by the new genus. It is possible that the plants may once have occurred here but became extinct owing to habitat degradation. There is little doubt that the unique habitat occupied by the bulbs is very vulnerable to degradation, particularly if new homesteads are built in the vicinity of the colonies.

There is a probability that the new genus has few or no natural predators. This is likely to be related to the strong garlic smell of all parts of the plant, except the flowers. The bulbs are likely to have insecticidal or insect-repelling properties, which may merit investigation. The factor most likely to control the numbers of plants is drought. In dry years, colonies of bulbs probably continue to thrive in the wettest parts of the seepage areas while plants in drier, less suitable areas, dry out. Many bulbs, particularly the very small, young ones, are likely to succumb.

Plants of this undescribed genus may well be adversely affected by the global warming predicted for the subcontinent. Ideally, data should be collected over several years to provide insight into the population dynamics of the plants during wet and dry years.

Zantedeschia jucunda, another endemic of the Leolo Mountains, occupies several distinct niches in this environment. This is likely to permit the plants to adapt to increasing aridity. These circumstances do not apply to the new genus, indicating the importance of studies on the autecology of specific bulbous plants growing on the mountain.

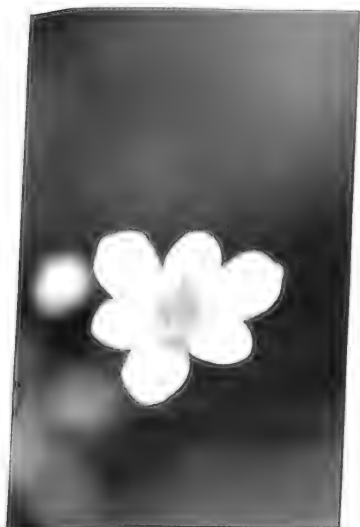


Fig. 4. Detail of the small but striking white flowers of the new genus.

It is highly unlikely that the new genus will be encountered in other parts of Sekhukhuneland, as the particular seepage areas where the plants are found are associated with norite outcrops at equivalent altitudes (above 1600 m) on the plateau of the Leolo Mountains. There are no other habitats in Sekhukhuneland that meet this criterion. However, in this respect the huge sheets of exposed norite near Phokwane northwest of Nebo in southwestern Sekhukhuneland should not be disregarded and may require botanical exploration. However, we speculate that these habitats will probably be too dry.

Taking into account the known information on the new genus, it can be deduced

that it is a narrow endemic restricted to a specific habitat. It has an area of occupancy of approximately 20 km² and, taking into account the trampling by cattle and recent housing developments, it was preliminarily assessed as Critically Endangered according to the IUCN 1994 criteria and is of conservation priority. The verification of this assessment is dependent on further research.

Readers are encouraged to contact Clare Archer (Private Bag X101 Pretoria 0001 Gauteng, South Africa; e-mail: clare@nbipre.nbi.ac.za) at the National Botanical Institute in Pretoria if they suspect that they have encountered the new genus.

ACKNOWLEDGEMENTS

We would like to thank Ms. Clare Archer and Dr. Robert Archer of the National Botanical Institute for their encouragement during our research and for discussions of aspects covered in the text. In particular we are grateful for their graciousness in permitting this paper to be submitted for publication while their taxonomic research on the new plant is still in progress. The University of Pretoria is thanked for funding the second author's studies in Sekhukhuneland through research funds managed by Professor Braam van Wyk. Ms Emsie du Plessis of the National Botanical Institute is thanked for proofreading the manuscript.

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All photographs by Connall Oosterbroek

***FRITILLARIA CHLORANTHA* (LILIACEAE),
AN ENDEMIC SPECIES IN IRAN**

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Although comparatively little has been written about *Fritillaria* in the past, the genus has been known for many centuries. The old Herbals show woodcuts of a number of species, which in many cases are not easily reconciled with names. According to Beck (1953) the earliest of these are probably Pena and Lobel (1570), and Gerarde (1636). The genus *Fritillaria* was established by Linnaeus (1753). In his *Species Plantarum*, he included four species, *F. imperialis*, *F. persica*, *F. meleagris* and *F. pyrenaica*.

Baker (1874), in his review of the genus, disposed the species in ten subgenera, of which three, *Rhinopetalum*, *Korolkowia* and *Notholirion*, are now sometimes accepted as distinct genera under the same names (cf. Losina-Losinskaya, 1935). My study on nectary morphology has also supported the separation of *Rhinopetalum* into a distinct genus (Bakhshi Khaniki and Persson, 1997). Bentham and Hooker (1883) reduced Baker's subgenera to five sections: *Eufritillaria* (incl. *Rhinopetalum*), *Ambliirion*, *Petilium*, *Theresia*, and *Liliorhiza*. Boissier (1884) reduced the first four of these sections to three, *Ambliirion* being submerged into *Eufritillaria*. The section *Liliorhiza* was not considered by Boissier as it does not occur in the Flora Orientalis area. After the exclusion of *Rhinopetalum*, *Korolkowia* and *Notholirion*, *Fritillaria* now comprises four subgenera, *Fritillaria*, *Theresia*, *Petilium*, and *Liliorhiza*.

Sixteen species of *Fritillaria* have been recorded from Iran, two of which were recently described, *F. atrolineata* Bakhshi Khaniki and *F. chlororhabdota* Bakhshi Khaniki. All Iranian species of *Fritillaria* belong to the subgenera *Petilium*, *Theresia* and *Fritillaria*. Of the four main groups within *Fritillaria* subg. *Fritillaria* in Western Asia and Europe, three occur in Iran: the *F. crassifolia* group, the *F. kotschyana* group and the *F. caucasica* group. *F. chlorantha*, the subject of the present investigation, belongs to the *F. caucasica* group.

F. chlorantha Hausskn. & Bornm. Figs 2-3. —Haussknecht & Bornmüller, Mitt. Thür. Bot. Ver. N.F. 20: 45 (1905). Type: Iran, "Luristaniae in monte Schuturunkuh", May 1897, Strauss (lecto. JE!). Ic.: Mathew, J. Roy. Hort. Soc. 90: Fig. 4 (1965). —Rix, Iran. J. Bot., Fig. 7 (1977). Rix & Phillips, The Bulb Book, p. 78, Fig. d-e (1981). —Mathew, The Smaller Bulbs, Fig. 40 (1987).



Fig. 1. *Fritillaria chlorantha* in flowering (original material was collected from Oshtorankuh, Iran).



Fig. 2. *Fritillaria chlorantha* in fruit (original material was collected from Oshtorankuh, Iran).

Bulb ovoid, up to 2.5 cm in diameter; bulbils present, few, without stolons. Stem 4–10(–17) cm, smooth. Leaves 4–10, usually 5, shiny green, all alternate; the lowest 5–10 x 1.2–5 cm, lanceolate to broadly lanceolate; the upper 5–6 cm long, linear-lanceolate. Flowers 1–2, \pm tubular; perianth segments green outside, mostly yellowish inside, the outer 15–30 x 3–6 mm, oblanceolate-oblong, obtuse; the inner somewhat wider. Nectaries 3–5 x 1–1.5 mm, linear-lanceolate to lanceolate, green, hardly depressed, not very distinct, placed at 1 mm above the base of the perianth segments. Filaments

5–7.5 mm long, yellowish green, papillose. Anthers (4–) 5–7 mm after dehiscence, yellow; pollen sculpture macroreticulate, exine surface smooth. Style 6–8 mm long, stout, 3-fid at apex for 1–1.5 mm, papillose. Ovary 3–4 mm long, stout. Capsule 3.5–5 cm long, cylindrical, not winged. Seeds 5.5–6.5 x 5–6 mm, ovate to subcircular in outline.

Chromosome number: $2n = 24$ (Bakhshi Khaniki, 1998).

Flowering time: April–May.

Ecology and distribution: Mountain steppe, among stones, 1800–3000 m and endemic to Iran. *Fritillaria chlorantha* is characterized by its short stems, broad shiny green leaves and usually bright green flowers, although specimens from two localities (BSBE 694–695) have tepals marked with purple. RIX (1977) suggested this may be a sign of hybridization with *F. zagrica* or *F. assyriaca* but I find this unlikely.

SPECIMENS EXAMINED

Lorestan: Oshtoran kuh, south of Thiun, north and east facing slopes, among stones, 2438 m, 27.4.1966, Archibald 1609 (GB, K); in Schuturunkuh, May 1897, Strauss (type material, JE). — *Arak*: Arak, Oshtoran kuh, May 1897, Strauss (JE); Aligudarz to Dow Rud, north of Thiun village, Oshtoran Kuh, 1900 m, 15.5.1994, Bakhshi Khaniki 88 (GB); Khorramabad, June 1897, Strauss (JE); foothills of Shuturankuh, north facing rocky and stony hillside, 1800 m, 7.4.1963, Mathew in BSBE 692, 694, 695 (K). — *Kordestan*: Kuh-e Dalaki, June 1910, Strauss (JE, type material); Pesandasht, 3000 m, 24.6.1936, Frödin (JE). — *Hamadan*: Elwand, 15.5.1895, Strauss (JE, W, type material).

NECTARY MORPHOLOGY

In *F. chlorantha*, the outer perianth segments are green outside, mostly yellowish inside, 15–30 x 3–6 mm, oblanceolate-oblong and obtuse. The nectaries are linear-lanceolate to lanceolate, 3–5 x 1–1.5 mm and green. They are hardly depressed and not very distinct. Warts grouped on short ridges



Fig. 3. *FRITILLARIA CHLORANTHA*. **A.** Nectary on outer tepal. **B.** Cells from nectary border on outer tepal (nectary to the left). **C.** Groups of warts and ridges on nectary margin (nectary to the right) and tepal surface. Scales: A, 500 micrometer; B, 100 micrometer; C, 50 micrometer.

are rather densely distributed on nectary margins and the tepal surface (Fig. 1). More details of the nectary are given by Bakhshi Khaniki and Persson (1997).

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THE *FRITILLARIA KOTSCHYANA* GROUP (LILIACEAE) IN IRAN

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ABSTRACT

Notes on taxonomy, morphology, ecology, nectary and karyology of the *Fritillaria kotschyana* group in Iran are presented. This group is morphologically characterized by having nodding, broadly campanulate flowers and lanceolate to ovate nectaries, less than half as long as the limb of the perianth segments, and located at the inflection of the bell (about 4–7 mm above the base of the tepals). It includes two species in Iran, *F. kotschyana* ssp. *kotschyana* and *F. olivieri*. They are morphologically similar to each other but differ by several minor characters. The flowers are green, suffused with reddish-brown or only lightly tessellated (not heavily tessellated), more or less distinctly margined with brown or purple outside. The leaves are narrowly lanceolate (not lanceolate to ovate), and the stem is papillose at ground level (not smooth). The styles are 3-fid and glabrous in both species. The flowering time for *F. kotschyana* ssp. *kotschyana* is April–July and the normal habit is rocky slopes and screes. The flowering time for *F. olivieri* is May–June and it grows in damp meadows by streams, sometimes at the edge of melting snow, and the border of fields. The somatic chromosome number of both species is $2n = 24$.

INTRODUCTION

The genus *Fritillaria* sensu lato belongs to the tribe Tulipeae of the Liliaceae. Of the four main species groups within *Fritillaria* subgenus *Fritillaria* in Western Asia and Europe, three occur in Iran. No member of the *F. meleagris* group has yet been recorded from Iran, but a representative of the group (*F. latifolia*) is found in neighboring areas of Turkey and the Caucasus, and is likely to be found in northern Azarbaijan in Iran (Rix, 1974, 1977). All Iranian species are classified into three subgenera: *Fritillaria*, *Theresia*, and *Petilium* (Bakhshi Khaniki, 1998). Subgenus *Fritillaria* is morphologically divided into three species complexes, the *F. crassifolia*, *F. meleagris*, *F. caucasica* and *F. kotschyana* groups (Rix, 1977; Rechinger, 1990). The aim of this paper is to present the latest data on taxonomy, morphology, ecology, and karyology of the *F. kotschyana* group.



Fig. 1. *Fritillaria kotschyana* ssp. *kotschyana*, Shemshak, Tehran, Iran.

TAXONOMY

Key to the Iranian species groups of subgenus *Fritillaria*:

1. Flowers broadly campanulate; nectaries ca. 5–7 mm above base of perianth segments 2
1. Flowers narrowly campanulate, rarely rounded (\pm urceolate); nectaries at or 0.2–2 mm above the base of perianth segments.....*F. caucasica* group
 2. Nectaries linear, more than half as long as the limb of the perianth segments*F. crassifolia* group
 2. Nectaries ovate to lanceolate, less than half as long as the limb of the perianth segments*F. kotschyana* group

Key to the Iranian species of the *F. kotschyana* group:

1. Flowers clearly tessellated, usually with fascia; leaves \pm ovate (2–4 times as long as wide)*F. kotschyana* ssp. *kotschyana*
1. Flowers obscurely tessellated, usually without fascia; leaves narrowly lanceolate (7–10 times as long as wide)*F. olivieri*

F. kotschyana Herbert ssp. *kotschyana* (Figs. 1–5). Herbert, Bot. Reg. 17: 43 (1844).

Type: Iran, “Persia borealis in regione alpina montis Elburs”, 13 July 1843, Kotschy 507 [neo. BM (Rix 1974); iso-neo. K!, G! —see nomenclatural note].

Ic.: Wendelbo, Tulips & Irises of Iran, Fig. 28 (1977). —Rechinger, Flora Iranica 165, t. 174, Fig. 4 (1990).



Fig. 2. *Fritillaria kotschyana* ssp. *kotschyana*, Golestan Province, Iran.

Nomenclatural note: This species was first described from cultivated plants grown by the Dean of Manchester, William Herbert, at Spofforth in 1844. He had received the bulbs from Kotschy, and Rix (1974), who had seen specimens collected by Kotschy in 1843, designated those at the BM as the neotype.

Bulb ovoid to subglobose, up to 3 cm in diameter, of two fleshy scales, without bulbils, stolons sometimes present. Stem 8–20(–33) cm tall, smooth. Leaves 3–8, green, all alternate, the lowest 6–10 x 1.5–3.5 cm, lanceolate to ovate, 2–4 times as long as wide. Flowers 1(2), broadly campanulate, tessellated brown-purplish inside and out on a green background, usually with green fascia; perianth segments 2.5–3.5(–4.5) x 1.5–2 cm, the outer broadly oblanceolate and obtuse, the inner somewhat wider. Nectaries ovate to ovate-triangular, 4–5 mm above base of perianth segments, 6–7 x 3–5 mm, dark purplish basally (green when immature), without a swollen ridge inside but instead deeply depressed, especially towards base, usually prominently protruding on the outside of the tepals, especially on outer tepals. Filaments 6–10(–13) mm long, brownish-yellow, densely papillose; anthers 5–5.5 mm long after dehiscence, yellow; pollen sculpture macroreticulate, exine surface smooth. Style 6–10(–13) mm long, 3-fid for 2.5–3 mm, glabrous. Ovary 4–5 mm long, stout. Capsule 16–22 mm long, obovoid, narrowly tapering toward the base, not winged. Seeds 6.5 x 5–5.5 mm, ovate in outline.



Fig. 3. Habitat of *Fritillaria kotschyana* ssp. *kotschyana*.

The flowers of *F. kotschyana* ssp. *kotschyana* usually have two color forms. The most common has large and distinct green fascia and rather obscure brown-purplish tessellation; the other has smaller and less clear fascia and is heavily tessellated. The name *F. kotschyana* has been used for dwarf plants of *F. latifolia* Willd. from northern Turkey, a very different species which has never been reported from Iran. Subspecies *kotschyana* has also been confused with *F. crassifolia* Boiss. & Huet, all subspecies of which are smaller and have a linear nectary. *F. kotschyana* ssp. *grandiflora* differs from ssp. *kotschyana* in the absence of fascia and is generally larger. Furthermore, the styles are papillose in ssp. *grandiflora* but glabrous in ssp. *kotschyana*. Ssp. *kotschyana* is related to *F. olivieri* but this species has flowers without fascia or tessellation.

Specimens examined:

Iran: *Mazendaran*: Gorgan, Kandovan pass, northern side, 2800 m, 24.6.1959, Wendelbo 2159 (BG, TARI); Gorgan, Haraz valley, Darli above Panjab, in forest, 2200 m, 11.5.1959, Wendelbo (BG, TARI); Gorgan, Haraz valley, Dehah, North of Panjab, in shrub-berry, 2150 m, 22.4.1959, Wendelbo 335 (BG, W); Gorgan, Jangal-e Loveh towards Dasht-e Shah, 1.5.1978, Daneshpajouh E-38643 (GB, E, TUH), 1800 m, 27.4.1994, Bakhshi Khaniki 99

(GB); Gorgan, Siahbisheh, Chalus valley, 2350 m, 16.4.1970, Foroughi 234 (GB, W, E); 2110 m, 11.5.1972, Sabeti 5654 (GB, E, TUH); Gorgan, Dasht-e Shah, 1.5.1978, Hallenberg (GB); Chalus road, near the watershed on Mazendaran side, 2000 m, 30.5.1934, Trott 210 (K); 8 km north of Kandovan Tunnel on Karadje–Chalus road, on rocky hillside, 2156 m, Ingham 175 (K), 1900–2300 m, 19.5.1994, Bakhshi Khaniki 102 (GB); central Elborz mountains, near Pol-e Zangule, Sabeti et al. 1566 (W, TUH); Chalus valley, above Siahbisheh, degraded forest, 2200 m, 23.5.1974, Wendelbo & Shirdelpur 11683 (GB, W, E, TARI), Tregubov 44 (W), 2100–2300 m, 18.5.1994, Bakhshi Khaniki 101 (GB); road of Gorgan to Bojnurd, Golestan forest, 1000 m, 26–27.4.1994, Bakhshi Khaniki 100 (GB). —*Gilan*: Asalem to Khalkhal, 25 km Khalkhal, Kouhshay-e Kerman, 1800–2100 m, 11.5.1977, Termeh & Matine E-36604 (W, E). —*Tehran*: north-east of Tehran, north slopes of Gachsar, 2500–2700 m, 19.5.1994, Bakhshi Khaniki 97 (GB), Gachsar to Chalus, 3000 m, 18.5.1956, Schmid 5738, 5739 & 5740 (G), above Gachsar, in stony, steep slopes and in damp earth slopes among large rocks, 2812 m, 8.6.1962, Furse 2529 & 2530 (K,

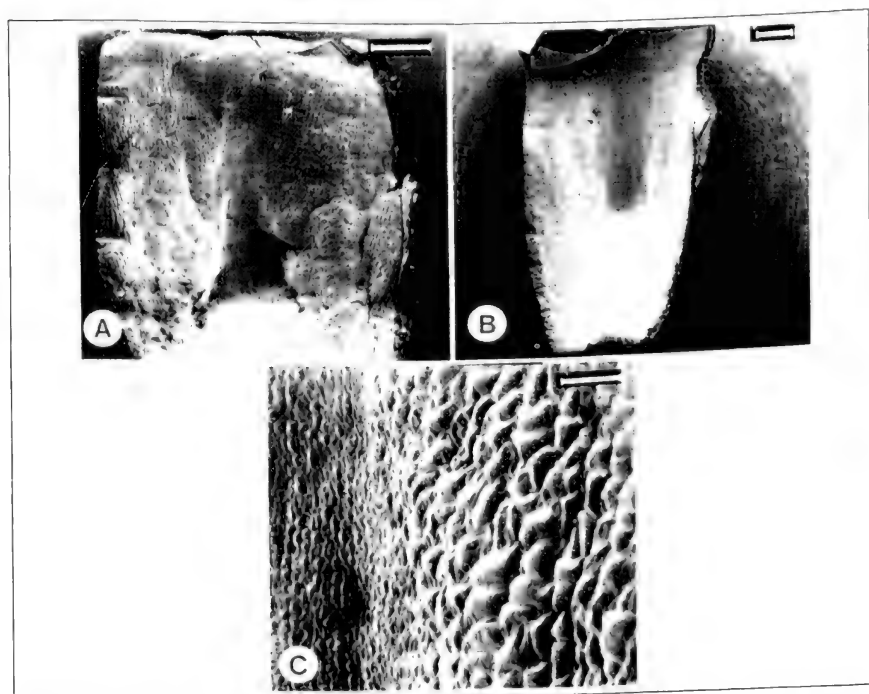


Fig. 4. SCANNING ELECTRON MICROGRAPHS OF *F. KOTSCHYANA* SSP. *KOTSCHYANA*. **A.** Nectary on outer tepal. **B.** Nectary on inner tepal. **C.** Cells from nectary border on outer tepal (nectary to the left). Scales: A-B: 1 mm; C: 100 μ m.

W); Shemshak, rocky and stony places, 2800 m, 8.5.1993, Bakhshi Khaniki 26 (GB), 20.5.1994, Bakhshi Khaniki 98 (GB), 23.5.1975, Wendelbo 17226 (GB, K); Elborz mountains, Tachti Soleiman area, near Piaschal, 3600–3700 m, 20.6.1902, Bornmüller 8281 (K, G); Elborz mountains, Hasartschal, 13.7.1843, Kotschy 507 (G, K, type material of *F. kotschyana*); 80 km north of Karaj, 2950 m, 10.5.1961, Stutz 1117 (W).

ECOLOGY

Flowering time: April–July.

Ecology and distribution: Rocky slopes and screes, usually at high altitudes, 1000–3700 m. Endemic to Iran (Fig. 3).

F. olivieri Baker (Figs. 6A–B), J. Linn. Soc., Bot. 14: 261 (1874). Type: Iran, Hamadan, “ad montem Elwand”, Olivier (holo. G-Boiss.!, iso. P!).

Ic.: Furse & Nowell, The Lily Year Book 27, Fig. 45 (1964). —Furse, J. Roy. Hort. Soc. 88: Fig. 70 (1963). —Rix, Iran. J. Bot. 1(2), Fig. 6 (1977). —Rix & Phillips, The Bulb Book, p. 93, Fig. j (1981). —Turrill & Sealy, Hooker’s Icones Plantarum 39 (1 & 2), t. 3818 (1980).

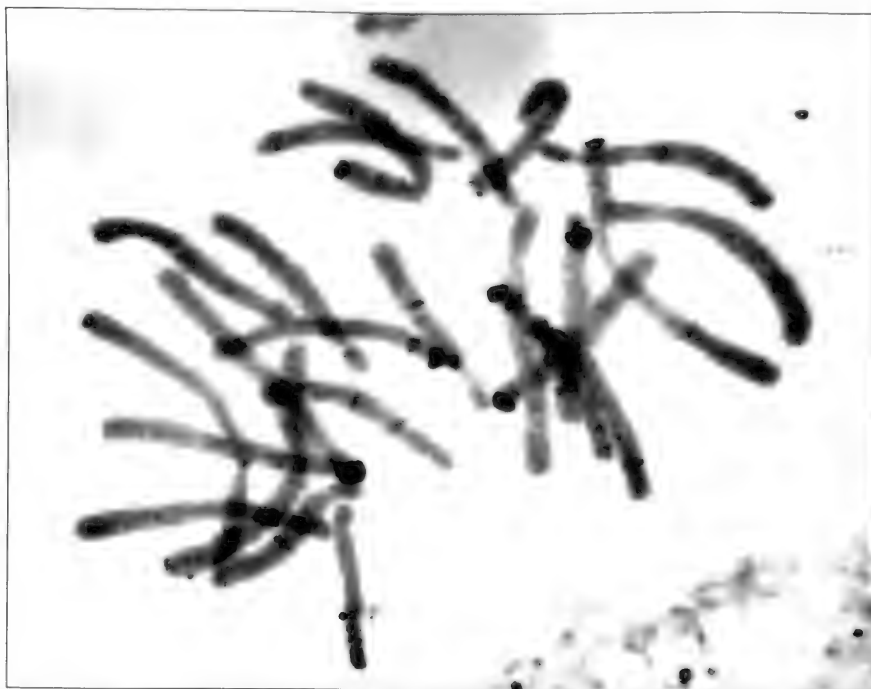


Fig. 5. *Fritillaria kotschyana* ssp. *kotschyana* somatic chromosome number, $2n = 24$.



Fig. 6. *Fritillaria olivieri* in flower.

Bulb subglobose, 2–3 x 3–4 cm, of usually 2 fleshy scales; bulbils few, without stolons. Stem 14–40(–56) cm, papillose at ground level. Leaves 5–10, usually 5–7, usually green but sometimes mildly glaucous, all alternate, the lowest 7.5–13 x 0.9–2 cm, 7–10 times as long as wide, narrowly lanceolate, the uppermost 3–5.5 x 0.1–0.4 cm, linear, acute. Flowers 1(–3), broadly campanulate; perianth segments green, \pm suffused or rarely lightly tessellated by red-

dish-brown, minutely papillose at apices; the outer 2.5–3.5 x 1.2–1.4 cm, obovate and obtuse; the inner somewhat wider (1.3–2 cm), obtuse.

Nectaries narrowly lanceolate to linear-lanceolate, rather flat and obscure at least in upper part, 5–6.5 x 2–2.5 mm, dark green, 7–9 mm above the base of the tepals. Filaments 8–11 mm long, sparsely papillose, yellowish. Anthers 5–9 mm long before dehiscence, yellow; pollen sculpture macroreticulate,



Fig. 7. *Fritillaria olivieri* in fruit.



Fig. 8. *Fritillaria olivieri* habitat.

exine surface smooth. Style 6.5–9 mm long, 3-fid for 1/4 to 1/3 of the length, glabrous. Ovary 8–10 x 2 mm, yellowish-green, stout. Capsule 4 cm long, obovoid, narrowly tapering toward the base, not winged. Seeds 6–6.5 x 4.5 mm, ovate in outline.

Chromosome number: $2n = 24$ (La Cour, 1978; Bakhshi Khaniki, 1998).

Specimens examined:

Iran: *Kermanshan*: Kermanshah, Kuh-e Parrow, 1908 m., Strauss (JE). —*Kordestan*: Noa Kuh, 2187 m, Strauss (JE); east of Sanandaj, beside a stream in damp meadows, 1875 m, 17.5.1962, Furse 2057 (W); Sanandaj to Hamadan, 40 km east of Sanandaj, Dasht-e Zaghagheh, 2000 m, 6.5.1994, Bakhshi Khaniki 59 (GB); road of Sanandaj to Marivan, Tiz Tiz pass, 1900 m, 5.5.1994, Bakhshi Khaniki 67 (GB); Ghorveh, Sanginabad village, Kuh-e Baghcheh Maryam, 1880 m, 5.5.1994, Bakhshi Khaniki 53 (GB). —*Hamadan*: Hamadan, Elwand mountain, 1900 m, Strauss (JE); Elwand mountain, above Ganjnameh, Pichler (K, G), 2100–2800 m, 30.4.1994, Bakhshi Khaniki 61 (GB); north-east face of Kuh-e Elwand, in deep granite soil, very porous and damp above stream, 2500 m, 13.5.1962, Furse 1985 (K, W); foothills of Elwand, in tall grass in moist conditions at the edge of a river, 19.5.1963, Mathew in BSBE 1666 (K); Elwand mountain, 1822, Olivier (G, P, type material); Pichler 96 (G); Rioux & Golvan 1721 (G, W). —*Eastern Azarbaijan*: Tabriz, mountain Heron,

May 1929, Gilliat-Smith 2493 (K). —*Lorestan*: Dow Rud, in damp meadow, 1875 m, 1.5.1941, Koelz 17482 (W); road from Dow Rud to Azna, Rostamghalah, in humid places with tall grasses, 1800 m, 14.5.1994, Bakhshi Khaniki 82 (GB); Dow Rud, 6.5.1994, Bakhshi Khaniki 59 (GB).

ECOLOGY

Flowering time: May–June.

Ecology and distribution: Damp meadows by streams, sometimes at the edge of melting snow and border of fields, 1750–2800 m. Endemic to Iran.

Fritillaria olivieri is similar to *F. kotschyana* but differs in several minor characters. The flowers are green, suffused in reddish-brown or only lightly tessellated (not heavily tessellated), \pm distinctly margined with brown or

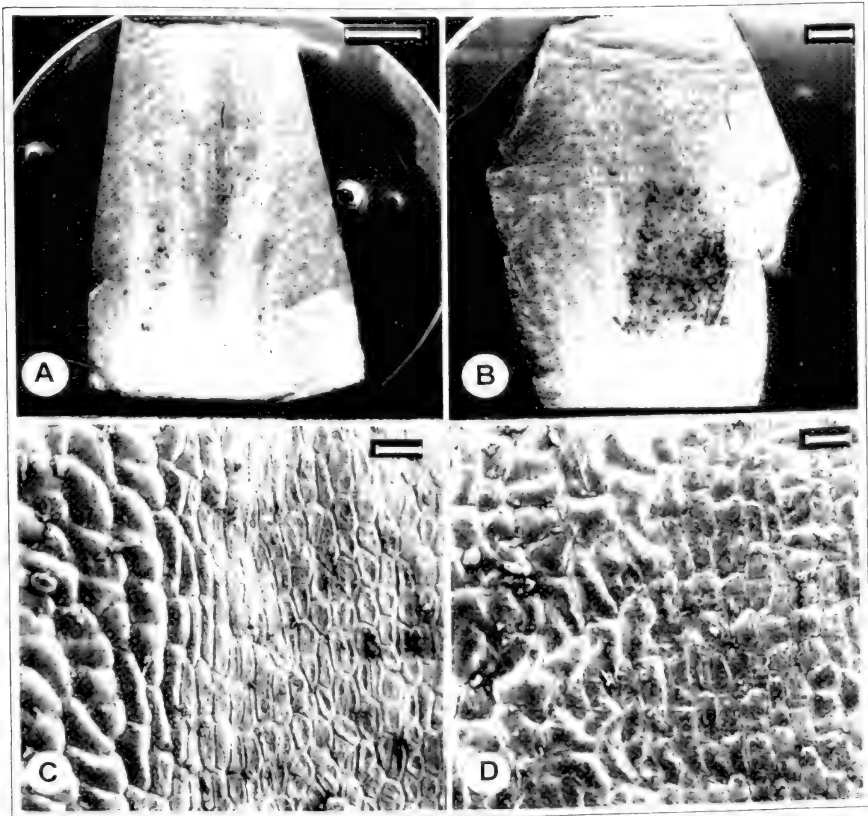


Fig. 9. *FRITILLARIA OLIVIERI*. A–D ELECTRON MICROGRAPHS OF NECTARY. **A.** Nectary on outer tepal. **B.** Nectary on inner tepal. **C.** Cells from nectary border on outer tepal (nectary to the right). **D.** Cells from nectary border on inner tepal (nectary to the right). Scales: A, 2 mm; B, 1 mm; C–D, 50 µm.

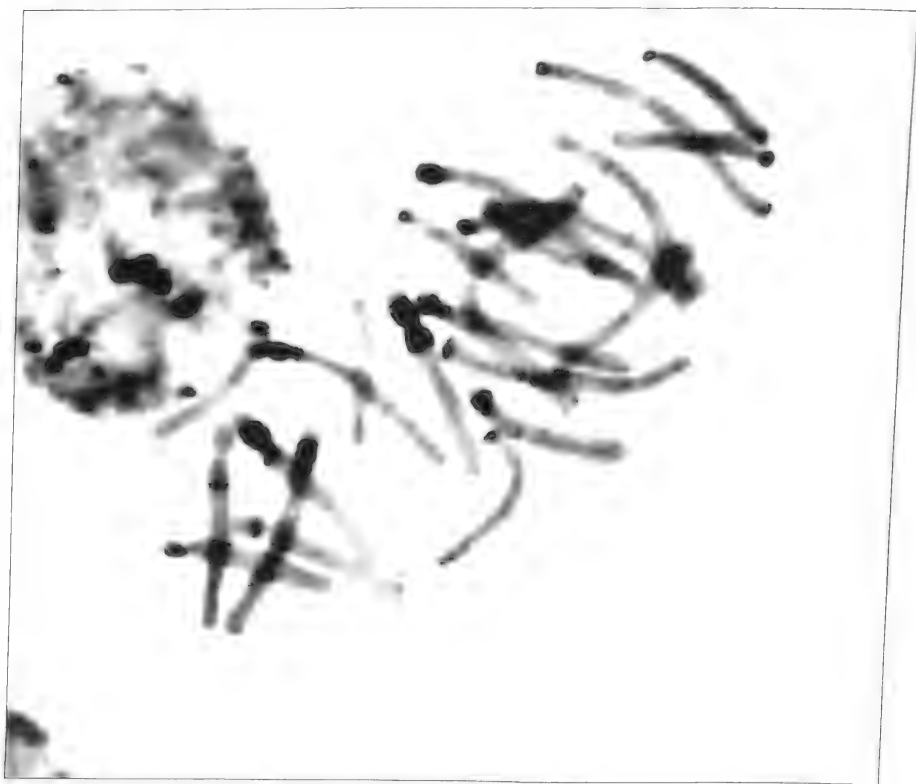


Fig. 10. *Fritillaria olivieri*. Mitotic metaphase $2n = 24$.

purple outside; the leaves are narrowly lanceolate (not lanceolate to ovate); and the stem is papillose at ground level (not smooth). The styles are 3-fid and glabrous in both species but the filaments in *F. kotschyana* ssp. *grandiflora* are long and very minutely papillose. Those of both *F. kotschyana* ssp. *kotschyana* and *F. olivieri* are rather short and densely papillose. According to Turrill and Sealy (1980), the morphological characters of *F. olivieri* are decidedly close to those of *F. pontica* Wahl (from N. Greece–N.W. Turkey), which has more rounded nectaries, however.

NECTARY MORPHOLOGY

The *Fritillaria kotschyana* group is characterized by having noddling, broadly campanulate flowers and lanceolate to ovate nectaries, less than half as long as the limb of the perianth segments, and located at the inflection of the bell (about 4–7 mm above the base of the tepals).

In *F. kotschyana* Herbert ssp. *kotschyana*, the nectaries are ovate to ovate-triangular, 6–7 x 3–5 mm, dark purplish basally (green when immature), and without a swollen ridge inside, but instead are quite depressed, especially towards the base. They stand out prominently on the outside of the tepals, especially those of the outer tepals (Fig. 3). In *F. olivieri*, the nectaries are narrowly and acutely lanceolate to linear-lanceolate, rather flat and obscure at least in the upper part, 5–6.5 x 2–2.5 mm, and dark green. Similarly to *F. kotschyana*, the tepal surface is not tuberculate in this species (Fig. 4).

KARYOLOGY

In *F. kotschyana* Herbert ssp. *kotschyana* the somatic chromosome number is $2n = 24$ and the haploid karyotype contains two metacentric, four subtelocentric and six telocentric chromosome pairs (Fig. 3). In *F. olivieri* Boissier the somatic chromosome number is also $2n = 24$, but the haploid karyotype consists of two large metacentric, five subtelocentric and five telocentric chromosome pairs (Fig. 3.)

ACKNOWLEDGEMENTS

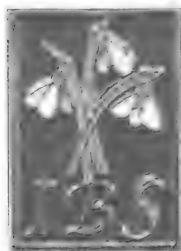
I wish to thank Dr. Karin Persson and Prof. Lennart Andersson (Botanical Institute, Göteborg University, Sweden) for reading the manuscript and helpful suggestions.

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***FRITILLARIA REUTERI* (LILIACEAE), A PECULIAR SPECIES
OF FRITILLARY IN IRAN**

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Of the four main species groups within *Fritillaria* subgenus *Fritillaria* in Western Asia and Europe, three occur in Iran. They are the *F. kotschyana*, *F. crassifolia* and *F. caucasica* groups. *F. reuteri* belongs to the *F. crassifolia* group.

F. reuteri Boiss. (Fig. 1A–C). Boissier, Diagn. Pl. Or. Nov. 1 (5): 57 (1844).

Type: Iran, "in Persia prope Esfahan", Aucher 5379 (holotype: G-Boiss., isotype: P!).

Icones: Furse, J. Roy. Bot. Soc. 94, Fig. 61–62 (1964). —Wendelbo, Tulips and Irises of Iran, Fig. 25 (1977). —Rix and Phillips, The Bulb Book, p. 86, Fig. c (1981). —Rechinger, Flora Iranica 165, t. 174, Fig. 2 (1990).

Bulb ovoid to subglobose, 12–15 x 13–14 mm, consisting of two fleshy scales; bulbils present, without stolons. Stem 14–25(–37) cm, smooth. Leaves 3–8, shiny green; the lowest 5.5–11 x 1.5–2.5 cm, alternate, linear-lanceolate, obtuse; the middle of stem leafless; the upper leaves narrower, 2.5–7 cm long, 2–3 at the base of each pedicel (opposite or whorled), linear. Flowers 1–4(–8), usually 1–2, broadly campanulate; perianth segments reddish-purple with a glaucous bloom, the apices 1/3–1/4 yellow inside and out, not tessellated; the outer 1.5–3 x 0.6–1 cm, oblanceolate, subacute; the inner ones wider (0.7–1.3 cm), often obtuse. Nectaries 9–11.5 x 1–1.7 mm, linear, green, slightly raised, placed ca. 5 mm above the base of the perianth segments. Filaments 7–10(–13) mm long, slender, yellow, glabrous. Anthers 5–7(–8) mm after dehiscence, yellow; pollen sculpture macroreticulate, exine surface smooth. Style 7–13 mm long, 3-fid for 2.5–3.5 mm, papillose. Ovary 6 mm long, pale green, stout. Capsule 3.5–4.5 cm long, obovoid, tapering toward the base, not winged. Seeds 7–8 mm long, ovate in outline.

Chromosome number: $2n = 24$ (Bakhshi Khaniki, 1998).

Specimens examined:

Iran: *Bakhtiari*: Chehel Dokhtaran Kuh, on wet ground by a rivulet, 3000 m, 2.6.1959, Wendelbo 1778 (BG, W, TARI); Cheshm-e Kuhrang, 2500 m, 31.5.1959, Wendelbo 964 (BG, TARI); Zagros mountains, valley at foot of Zard kuh gorge, in very wet gravelly soil alongside stream, 30.5.1973, Hewer 2090 (GB). —*Lorestan*: 75 km east of Aligudarz, 1800 m, 17.5.1994, Bakhshi Khaniki

92 (GB). — *W. Azarbaijan*: Urmiah, 20 km east of Urmiah, Kuh-e Sir, between Sir and Pirhadi village, 2100 m, 13.5.1994, Bakhshi Khaniki 94 (GB). — *Esfahan*: Esfahan, Aucher 5379 (type material, holo. G-Boiss, iso. P), Esfahan, 75 km east of Aligudarz, 2300 m, in very wet meadow, occurring by the thousands, 2.5.1975, Wendelbo and Assadi 16410 (GB, W, TARI, TUH); Khunsar, Golestankuh, by stream, in wet meadow, 2600–2800 m, 2.5.1975, Wendelbo and Assadi 16396 (GB, W, TARI), 15.5.1994, Bakhshi Khaniki 91 (GB); 10–15 km north-west of Daran along road to Arak, in boggy ground, 2343 m, 2.5.1975, Ingham 143 (K); Shah-Kord, valley at foot of Zard Kuh gorge (Zagros mountain range), in very gravelly soil alongside stream, 2200 m, 30.5.1973, Hewer 2090 (K); road of Khunsar to Daran, south-east of Damaneh, Cheheldokhtaran Kuh, 2900 m, 14.5.1994, Bakhshi Khaniki 93 (GB).

Note: The living material of the populations collected by the author is cultivated now at the Botanical Garden of Göteborg, Sweden

ECOLOGY

Flowering time: May–June.

Ecology and distribution: Rocky meadows, along streams, usually very wet at flowering time, between 1800–3000 m.

Fritillaria reuteri is endemic to Iran. It is not a very variable species; however, on several occasions pure yellow flowers have been recorded



Fig. 1. *Fritillaria reuteri*. Sample collected from Golestan Kuh, Khunsar, Esfahan province.

(Freedman and Jones, 1969). According to Rix (1977), the species is restricted to the mountains north and west of Esfahan province, but I have found it from Kuh-e Sir in Urmiah (W. Azarbaijan), where it occurs in a few localities but in great quantity. The leafless intervening stem is unusual for the genus. It is similar to *F. michailovskyi* from Turkey in flower color, but *F. reuteri* has glabrous filaments as opposed to papillose in *F. michailovskyi*.

NECTARY MORPHOLOGY

The *Fritillaria crassifolia* group is distinguished by having usually broadly campanulate flowers (narrowly campanulate in *F. poluninii*), generally nodding at maturity, and linear nectaries, half or more than half as long as the perianth segments and placed at 3–5 mm above their base. The nectaries are usually black-purplish at the base, continuing and tapering toward the tepal apex by a narrow zone divided longitudinally by a channel. The basal part of the nectary is apparently more active in nectar sugar secretion because that is usually filled with a watery fluid which seems to trickle along the median furrow, i.e. downwards in the hanging flowers (Fig. 2). In *F. reuteri*, the outer perianth segments are 15–30 x 6–10 mm, oblanceolate, and subacute; the inner ones are wider, often obtuse. In color, they approach the former species. The linear, green nectaries are slightly raised, 9–11.5 x 1–1.7 mm and placed ca. 5 mm above the tepal bases. Similarly to *F. crassifolia* ssp. *poluninii*, warts and other vestiture are



Fig. 2. *Fritillaria reuteri*. Sample collected from Golestan Kuh, Khunsar, Esfahan province.

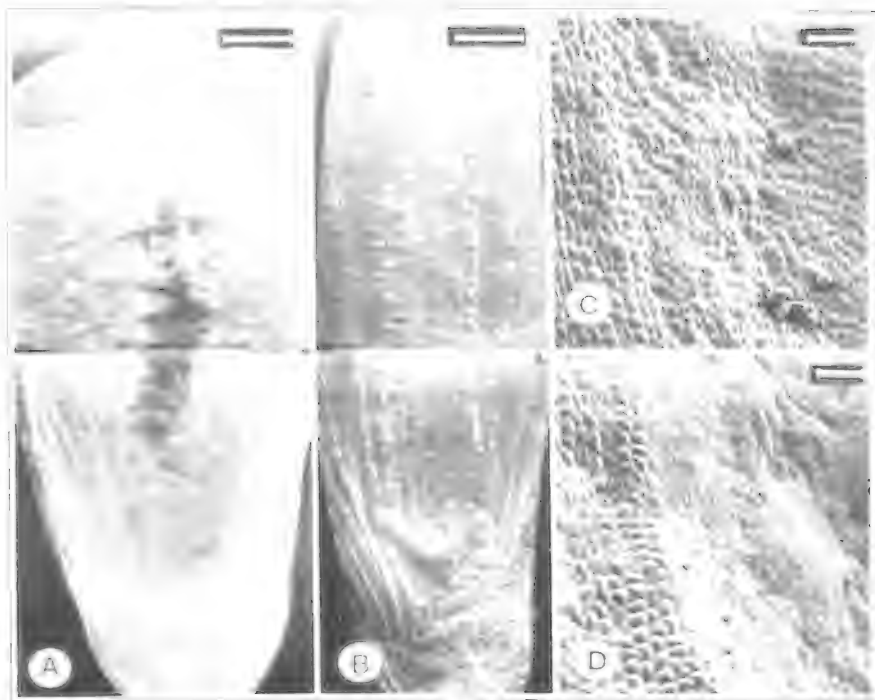


Fig. 3. SCANNING ELECTRON MICROGRAPHS OF *FRITILLARIA REUTERI*. **A.** Nectary on outer tepal. **B.** Nectary on inner tepal. **C.** Cells from nectary border on inner tepal (nectary to the right). **D.** Cells from nectary border on outer tepal (nectary to the left). Scales: A–B: 1 mm; C, 200 micrometer; D, 100 micrometer.

absent. More details about nectary morphology in southwest Asian *Fritillaria* (*Liliaceae*) is given in Bakhshi Khaniki and Persson (1997).

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MORPHOLOGY AND TAXONOMY OF *RHINOPETALUM* (LILIACEAE) IN IRAN

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ABSTRACT

Morphology and taxonomy of *Rhinopetalum* in Iran is presented, including a key, synonyms, descriptions, taxonomic comments, ecology, and citation of specimens examined. *R. gibbosum* (Boiss.) Losinsk. & Vved., and *R. arianum* Losinsk. & Vved. occur in Iran.

INTRODUCTION

Rhinopetalum was proposed by Fischer, but valid publication was accomplished by Alexander (1830). Baker (1874) treated *Rhinopetalum* as a subgenus of *Fritillaria*. Boissier (1882) did not accord any infra-generic status to this group of species and simply included it in his subsect. *Olostyleae* of *Fritillaria*. *Rhinopetalum* was revived as a separate genus by Losina-Losinskaya (1935) in the Flora of the U.R.S.S., who distinguished it from *Fritillaria* mainly on nectary characters. She recognized five species in the genus, namely *R. karelinii* Fisch., *R. gibbosum* (Boiss.) Los.-Losinsk. and Vved., *R. arianum* Los.-Losinsk. and Vved., *R. stenanthum* Regel, and *R. bucharicum* (Regel) Los.-Losinsk., of which, *R. arianum* and *R. gibbosum* occur in Iran. Because of the characteristic structure of the nectaries in *Rhinopetalum* as revealed by the scanning electron microscope (SEM), and also its general divergence from other fritillaries, segregation of subgenus *Rhinopetalum* from *Fritillaria* into a distinct genus was supported again by Bakhshi Khaniki and Persson (1997).

Eighteen species of *Fritillaria* and *Rhinopetalum* have been recorded from Iran, two of which were recently described, *F. atrolineata* and *F. chlororhabdota* (Bakhshi Khaniki, 1997a, 1997b), and one raised from sub-specific level, *F. poluninii* (Rix) Bakhshi Khaniki and K. Persson (Bakhshi Khaniki and Persson, 1997). Rix (1977) and Rechinger (1990) have disposed all Iranian species in four subgenera: *Fritillaria*, *Theresia*, *Petilium* and *Rhinopetalum*, of which the later is now accepted by some authorities as a distinct genus under the same name (Losina-Losinskaya, 1935; Bakhshi Khaniki and Persson, 1997).

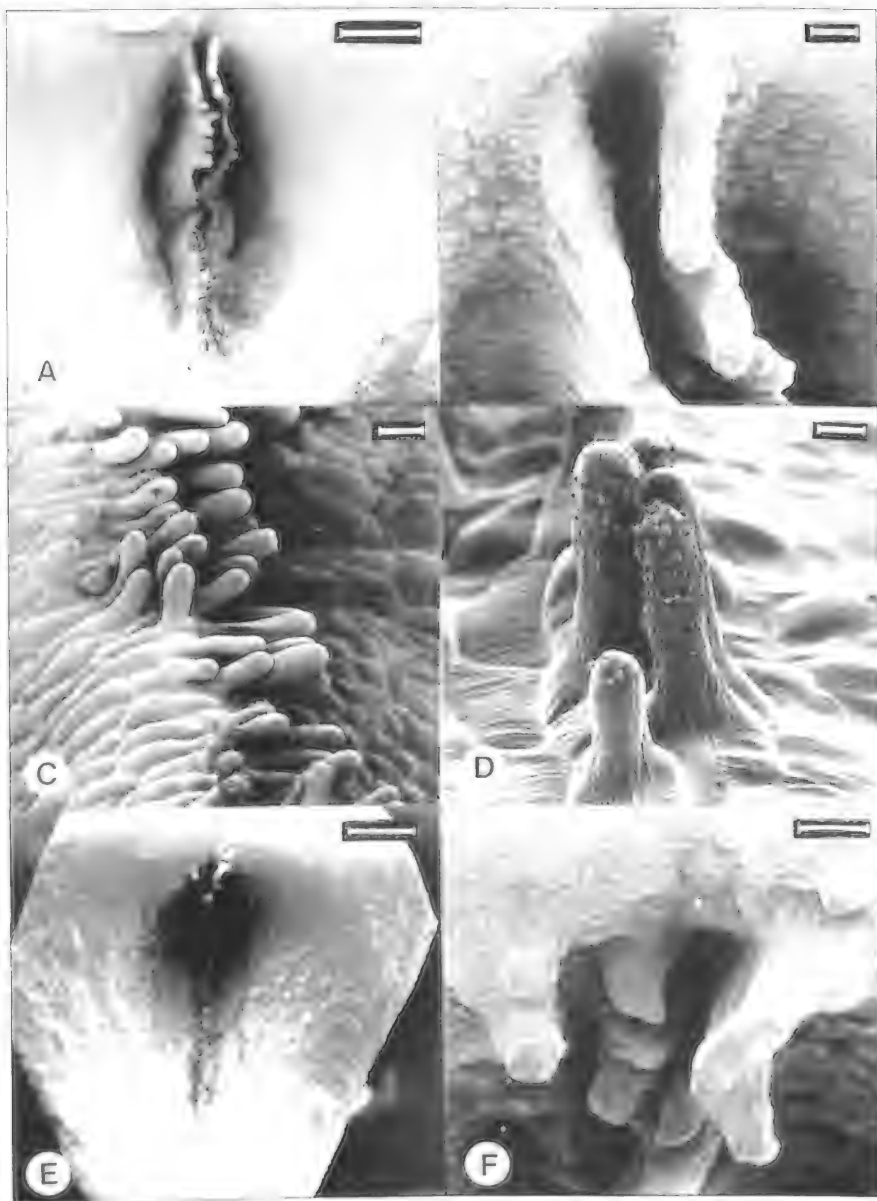


Fig. 1. A–D. *RHINOPETALUM GIBBOSUM*. A. Nectary on outer tepal. B. Fringed lobes in upper part of nectary. C. Hairs in lower part of nectary. D. Detail of hairs. E–F. *R. ARIANUM*. E. Nectary on outer tepal. F. Fringed lobes in upper part of nectary. Scales: A, E, 1 mm; B, F, 100 μ m; C, 50 μ m; D, 20 μ m.

The aim of the present investigation is to produce a modern morphologic and taxonomic revision of *Rhinopetalum* in Iran, using as much data as possible with the aid of light microscopy (LM) and scanning electron microscopy (SEM)

MATERIAL AND METHODS

In addition to material collected by the author from the field, material from the following herbaria was also examined (abbreviations according to Holmgren et al., 1990): BG, E, G, GB, JE, K, TARI, TUH, W. Fifteen species were also studied in the field in Iran (the collected living material is cultivated at the Göteborg Botanical Garden, Sweden), and another three were seen live in cultivation. Voucher specimens are kept in GB. The material was studied and measured under a stereo microscope. Nectaries, stamens, styles and seeds of all species were also studied using a scanning electron microscope. For this purpose, samples taken from fresh material then fixed and stored in FAA were critical-point dried and coated with a 50 Å layer of gold-palladium. The following informative characters were judged for morphologic and taxonomic studies: 1) bulb morphology, 2) stem and habit, 3) leaf number, shape, color and position, 4) inflorescence, 5) flower color and morphology, 6) nectary morphology, 7) androecium, 8) pollen morphology, 9) gynoecium morphology, 10) fruit morphology, and 11) seed morphology. Descriptions, and notes on habitat and elevation refer to Iranian material.

MORPHOLOGY

Bulbs. Bulb characters are invaluable for generic and sometimes for specific differentiation. The bulb usually consists of 2, sometimes 3 or 4, fleshy, subglobose scales, more or less tunicated by the marcescent remains of the scales of previous years.

Stems and habit. Flowering stems are erect and terete, with 1/3 of the stem usually subterranean, mostly unridged and glabrous, sometimes densely papillose. The stems vary considerably in height and robustness, even in the same population and in the same plant from year to year. The stems are frequently suffused with deep anthocyanin purple, especially the proximal portion. In some species they are markedly glaucous.

Leaves. In all species so far examined, very young plants have a single green leaf which is generally different in size and shape from the cauline leaves of the adult flowering stem. Usually it is broader, elliptic or lanceolate to ovate, and narrowing below into a long or short petiole. General leaf-shape is rather constant, but there is often considerable variation in size.

The arrangement (alternate, opposite, whorled) of the cauline leaves on the stem is of considerable taxonomic importance. Leaves usually occur from a little below the middle of the stem (\pm at ground level) up to the first flower. In single-flowered stems they cease at some distance below the perianth. Leaf color (glaucous or green) is also of diagnostic value. Most species have glaucous leaves, while they are shiny green in others.

Inflorescence. The genus *Rhinopetalum* has up to 11 flowers in a terminal raceme, with two bracts subtending each flower.

Flowers. The general shape of the perianth is most important taxonomically. The outline of the flowers depends on the relative length and breadth of the tepals, the degree of differentiation of the outer and inner tepals, the spread of the tepals, and the size, shape and depth of the nectaries.

The flowers of some species of *Rhinopetalum* are regular and actinomorphic with the normal formula for the *Liliaceae*. They are often drooping, usually hanging quite or nearly parallel to the stem. The pendulous position is said to protect the nectaries from being washed out by rain. Generally, the flowers are narrowly campanulate. Many of the species have a slight to fairly strong odor. The flower in some species of *Rhinopetalum* (*R. arianum*, *R. gibbosum*) is irregular and zygomorphic due to unequal nectary-projections in different perianth segments. Tessellation on the perianth is characteristic of *Rhinopetalum*, although it is lacking in some species.

Nectaries. In *R. gibbosum* flowers are flattish and zygomorphic. The outer perianth segments are about 15–20 x 7–10 mm and pink-tessellated. The nectaries are strongly calcarate, the upper larger than the others, and placed ca. 0.5 mm above the base of the perianth segments. Nectaries of the outer tepals are also much more deeply impressed than those of the inner series. The orifice of the nectaries is ca. 3–5.5 mm long and bound by two broad, fringed, purplish-brown lobes, which are densely and shortly ciliate in their lower parts (Fig. 1 A–D).

In the Turkmenian-Afghanian species *R. arianum*, flowers are rather similar to the preceding species but with outer perianth segments about 22–26 x 7–10 mm and finely and irregularly pink-spotted rather than tessellated. The nectaries are rather similar in type, about 3–4 mm long at the orifice, and placed ca. 0.5 mm above the base of the perianth segments. As opposed to *R. gibbosum* and *R. karelinii*, however, the two lobes surrounding the nectary orifice are very narrow, though they are distinctly fringed and ciliate (Fig. 1E–F).

More information in detail about nectary morphology and its taxonomic

implications in *Fritillaria* and *Rhinopetalum* is given in Bakhshi Khaniki and Persson (1997).

Androecium. The surface structure of the filament (papillose or glabrous) is taxonomically important and useful for subgeneric classification. All *Rhinopetalum* species have more or less papillose filaments. Shape, size and color of the filaments seem taxonomically unimportant, however.

Gynoeceum. The ovary is three-carpellate and three-locular. Taxonomists have laid considerable stress on the branching and structure of the style. On the whole, this organ seems to give very valuable characters. Among *Rhinopetalum* species, the styles are papillose in *R. stenanthum*, but glabrous in the rest of the species.

Fruit. The fruit in *Rhinopetalum* is a three-valved loculicidal capsule. Longitudinal dehiscence occurs down the center of the outer walls of the three compartments or locules. The general shape of the capsule, as well as the acute or obtuse, rounded or even slightly winged angles of the mature fruit are of taxonomic importance. Among *Rhinopetalum* species both winged and wingless capsules can be found.

Seed. The seeds are numerous in each capsule, disc-shaped with a flat rim. Generally, the outline of the seeds is elliptic to ovate. There are some differ-

ences in shape and size of testa cells among different species, but these differences do not seem to be very important taxonomically.



Fig. 2. *Rhinopetalum gibbosum*.

TAXONOMY

Key to the genera

1. Flowers actinomorphic; nectaries shallow, linear to lanceolate or ovate (rarely circular); pollen sculpture foveolate to reticulate..
Fritillaria L.
2. Flowers in some species zygomorphic; nectaries deeply depressed, shown as dark hump-like or sac-like projections on the outside of the segments; pollen sculpture usually regulate
Rhinopetalum Fisch. ex Alexand.



Fig. 3. *Rhinopetalum gibbosum*.

Rhinopetalum Fisch. ex Alexand.,
Edinb. New Phil. J. 8: 19 (1830).
Fritillaria subgen. *Rhinopetalum*
(Fisch. ex Alexand.) Baker, Journ.
Linn. Soc. 14: 253 (1874).

Type species: *R. karelinii* Fischer
ex D. Don in Sweet, Brit. Flow.
Gard. 6 (Ser. 2, 3): t. 283 (1835). —
Type LE (n.v.).

**General description of Iranian
species:** Bulbous perennials; bulb
usually of 2, sometimes 3 or 4 fleshy
or farinaceous subglobose scales, \pm
tunicated by the marcescent
remains of scales of the previous
year or years. Stem erect, smooth or
papillose. Leaves usually glaucous,
opposite to alternate, linear, lanceo-
late to ovate. Flowers nodding or \pm
horizontal at maturity, 1–7 or more
in racemes. Perianth zygomorphic
or actinomorphic, cup-shaped or

bell-shaped. Nectaries deeply depressed, appearing on the outside of the
tepals as dark hump- or sac-like projections, equal in some species, unequal
in others, nectary orifice bordered by two \pm fringed, purplish-brown lobes,
which are densely short-ciliate at least basally in. Filaments \pm papillose.
Anthers basifixed. Pollen monocolpate, often rugulate. Style glabrous, entire,
slender. Ovary 6-angled. Fruit a \pm depressed-globose capsule, winged or
wingless, narrowed into a stipe. Seeds numerous, discoid, ovate in outline,
with a wide flat margin.

Key to Iranian species of *Rhinopetalum*

1. Perianth segments distinctly pink-tessellated; nectary lobes broad; filaments very
minutely papillose at base *R. gibbosum*
2. Perianth segments finely pink-spotted; nectary lobes very narrow; filaments
densely papillose at base *R. arianum*

Rhinopetalum gibbosum (Boiss.) Los.-Losinsk. and Vved. in Komarov, Fl.
U.R.S.S. 4: 297 (1935) —Fig. 2–3. *Fritillaria gibbosa* Boissier, Diagn. Pl. Nov.

1 (7): 107 (1846). — *F. karelinii* Fisch. f. *gibbosa* (Boiss.) Bornmüller, Pl. Strauss., Beih. Bot. Centralbl. 24: 99 (1908). Type: Iran, "Schiraz, in declivibus prope ruinas Persepolis", April 1842, Kotschy 827 (holotype: G-Boiss., isotype: P!). *F. pterocarpa* Stocks, Hooker's J. Bot. 4: 180 (1852) (n.v.). Ic.: Furse and Nowell, The Lily Year Book 27, Fig. 42 (1964). — Mathew, J. Roy. Hort. Soc. 99: Fig. 11 (1965). — Wendelbo, Tulips and Irises of Iran, Fig. 26 (1977). — Rechinger, Flora Iranica 165, t. 173, Fig. 4 (1990).

Bulb narrowly ovoid to subglobose, up to 3 cm diameter, consisting of two fleshy scales; without bulbils or stolons. Stem 7–17(–25) cm, densely papillose, especially at base. Leaves 4–10(–12), usually opposite, glaucous; the lowest 3.5–7 x 1–2 cm, lanceolate to ovate; the upper shorter and much narrower than the lower, linear, acute; bract leaves linear, acute, usually 2 at the base of each pedicel. Flowers 1–7(–10), nodding at maturity, zygomorphic. Perianth segments 15–20 x 7–10 mm, \pm pink-tessellated, with many dark nerves, darker at the base, ovate-lanceolate; the outer somewhat narrower than the inner. Nectaries placed ca. 0.5 mm above the base of the perianth segments, ca. 3–5.5 mm at orifice, the upper larger than the others, strongly calcarate, bordered by two broad, fringed, purplish-brown lobes, which are densely short-ciliate basally; nectaries of the outer tepals much more deeply impressed than those of the inner series. Filaments (5–)8–10 mm long, usually purplish, slender, minutely papillose toward base. Anthers 2–2.5 mm long, broadly oblong, purplish; pollen sculpture rugulate. Style 6–13 mm long, slender, entire, glabrous, pale purplish. Ovary 5–6 mm long, cylindrical, 6-angled. Capsule 10–16 mm long, subglobose, winged, toothed at top. Seeds 4.5–6 x 2–3 mm, ovate in outline. Chromosome number: $2n = 24$.

Flowering time: Early March–May.

Ecology and distribution: Stony slopes, steppes, bare rocky soil, rounded clay hills, 625–2050 m. Also known from Turkomania, Afghanistan, Pakistan and S. Transcaucasia.

Rhinopetalum gibbosum is a rather widespread species in Iran. It is rather variable both in number and color of the flowers. It resembles *R. arianum* in the shape of the perianth segments and in general shape of the nectaries, but differs in having a checkered pattern on its perianth, wide nectary lobes (Bakhshi Khaniki and Persson, 1997), and only minutely papillose filaments.

Specimens examined:

Iran: *Tehran*: road from Tehran to Karaj, Park-e Chitgar, 1350 m, 23.3.1993, Bakhshi Khaniki 1 (GB); Lashkarak towards Afgeh, Kuhhay-e



Fig. 4. *Rhinopetalum arianum*.

Närun, 1550–1750 m, 30.4.1976, Termeh and Matin 34905 (W, E), 1550 m, 29.3.1993, Bakhshi Khaniki 2 (GB); Mardabad, south of Karaj, frequent on hills, 1200 m, 30.3.1976, Wendelbo et al. 19047 (GB, TARI), 1350 m, 3.4.1993, Bakhshi Khaniki 3 (GB); Karaj, Ravandeh, 5.4.1934, Maula 8022 (GB, E), Gauba et al. 1565 (W); ridge north-west of Qum lake on road from Tehran, stony slopes, 1350 m, 30.3.1975, Wendelbo and Assadi 15291 (GB, TARI); west sides of road from Tehran to Qum, 5 km north of Kushk-e Nusrat, 1219 m, 31.3.1969, Hewer 905 (K); Elborz mountain, south side of watershed between Qazvin and Rasht, in rocky slopes, 625 m, 18.3.1962, Furse 1100 (K); Qazvin, Karaj, in mountain near the village Kalak, 1600 m, Rechinger 2746, 37594, (G, GB, W); Tehran to Arak, 41 km from Arak, 1350 m, 21.5.1993, Bakhshi Khaniki 32 (GB). —*Khorasan*: between Bojnurd and Shirvan, in clay, 1000 m, 20.4.1967,

Rechinger 33182 (W); south east of Fariman, 1350 m, 21.4.1967, Rechinger 33204 (W); 62 km south of Sabzevar, road of Kashmar, 1500 m, 19.4.1976, Rejamand and Bazargan 31674 (W, TUH); Kuhhay-e Nishabour, 1800 m, 30.5.1948, Rechinger 7324 (W, TUH); 14 km east of Bojnurd, 980 m, 15.5.1966, Rioux and Golvan 7881 (G); Quchan to Sultanabad, stony slopes below igneous cliffs, 1800 m, 8.4.1964, Furse 5218 (GB, K); 24 km north of Quchan, Kopet Dagħ, in sandy calcareous soil among *Artemisia*, *Umbelliferae*, *Leguminosae*, 2000 m, 19.5.1966, Furse 7520 (K); Kopet Dagħ range, 30 km west of Darreh Gaz and 40 km north east of Quchan, on N-facing slope of immature rocky soil, 1900 m, 21.4.1871, Gibbons 56 (K); Torbat-e Haydariyah, Robat Safid, 1800–2000 m, 27.5.1948, Rechinger 4459 (W); Bojnurd, Chaman Bid, 1500 m, 19.4.1967, Rechinger 33179 (W); road

from Bojnurd to Gorgan, before Rabatcharbil village, 1050–1250 m, 7.4.1993, Bakhshi Khaniki 4 (GB). —*Mazandaran*: Gorgan, Golestan forest, near Bojnurd road, along side road to Bakadeh, in *Artemisia*-steppe, 1250 m, 2.5.1974, Wendelbo et al. 11074 (GB, TARI), 1800 m, 2.5.1993, Bakhshi Khaniki 17 (GB); Gorgan, Shah Pasand to Shahrud, south side of pass, in *Artemisia* steppe, 3.5.1974, Wendelbo et al. 11141 (GB, TARI); 1950–1800 m, 18.5.1978, Wendelbo and Assadi 29678 (GB, TARI); Gorgan, towards Bojnurd, 106 km from Shahpasand, 1120–1300 m, 22.5.1976, Termeh and Matin 34889 (W, E). —*Azarbaijan*: 14 km south of Khoy on road to Shahpur, 1200 m, hills with sterile soil partly without vegetation, partly with *Artemisia*, 24.4.1976, Wendelbo and Assadi 19261 (GB, TARI, TUH); 20 km south west of Jolfa on road to Evaghli, soil slopes, 1100 m, 22.4.1976, Wendelbo and Assadi 19236 (GB, TARI); 50 km after Zanjan on road to Tabriz, stony ground, 1350 m, 20.4.1976, Wendelbo and Assadi 19177 (GB); Khoy, on rocky hillside in full sun, 4000 m, Mathew in BSBE 519 (K); **Tabriz**, 1928, Gilliat-Smith 2212 (K). —*Hamadan*: Hamadan, south east of **Roan**, 1845 m, among *Hultheimia* on low, rounded clay ridges, 11.5.1966, Archibald 1792 (GB); Aq Bulaq, c. 100 km north of Hamadan, 15.4.1960, Rioux and Golvan 11 (W, G); Aq Bolagh Morched, 60 km from Bijar, 24.4–10.5.1956, Schmid 6706 (G). —*Arak*: Arak to Golpaigan, 40 km east of Arak, 2031 m, 23.4.1962, Furse 1571 (K, W); Arak (Sultanabad), 20.5.1895, Strauss 49 (G).

Afghanistan: *Harat*: between Obeh and Khodja Chist near Pardu Kham (bulbs cultivated at Göteborg Botanical Garden, Sweden), 10.5.1969, Hedge, Wendelbo and Ekberg, W-7771 (BG); Istalif, 3.4.1958, Lindberg 398 (BG); Salzak pass on road from Herat to Qala Nau, mountain at start of pass, stony slopes, 2150 m, 16.5.1969, Hedge, Wendelbo and Ekberg W-8075 (GB); Harat, 1400 m, 1.4.1949, Köie 3565 (W). —*Logar*: Logar valley, in wheat field, 18.4.1968, Jørgensen 450 (GB). —*Fariab*: near Kawlyan, east of Belcheragh, soil slopes, 1200 m, 26.5.1969, Hedge, Wendelbo and Ekberg W-8391 (GB). —*Baghlan*: Mirza Antibili pass, soil slopes, 1450 m, 31.5.1969, Hedge, Wendelbo and Ekberg W-8551 (GB). —*Zabul*: 20 km north-west of Shenkay, Qlati-e Ghilzai, 2170 m, 25.3.1971, Podlech 20094 (G). —*Urgun*: 35 km north-west of Urgun, towards Surmat, 2200–2400 m, 10.6.1967, Rechinger 35934 (W); Urgun, April 1970, Rechinger 88 (W). —*Kataghan*: Paigah Kotal, Pul-e Khumri, 1500 m, 5.5.1967, Rechinger 33942 (W). —*Chisht*: 1600 m, 20.4.1949, Köie 4289 (W). —*Kabul*: Istalif, north of Kabul, 1900 m, 3.4.1964, Neubauer 4025 (W); Logar valley, in steppes, 2.5.1951, Volk 1839 (W).

Pakistan: *Quetta*: Spin Karez, 1800 m, 31.3.1965, Rechinger 27340 (W); in jugo W Ziarat, 2200 m, 12.5.1965, Rechinger 29331 (W); between Qila Abdullah and Sheila Bagh, 1600–1900 m, Rechinger 29040 (W).

R. arianum Los.-Losinsk. et Vved. Komarov, Fl. U.R.S.S. 4 (Addenda 3): 738 (1935). —Fig. 4–5. *F. ariana* (Los.-Losinsk. and Vved.) Rix, Iran. J. Bot. 1(2): 82 (1977). Type: “In arena mobili, in declivibus arenosis. Asiae Mediae” (not seen). Icones.: Losina-Losinskaya, Fl. U.R.S.S. 4: 299 (1935).

Bulb globose to subglobose, up to 2.5 cm diameter, consisting of two fleshy scales; bulbils or stolons absent. Stem 10–20(–40) cm, smooth, or papillose only below the lowest leaves. Leaves 8–10(–11), glaucous; the lowest 11–16 x 10–13 cm, linear-lanceolate, opposite to subopposite, acute; upper stem leaves alternate, linear; bract leaves 18–37 x 2–3 mm, linear, 2 at the base of each pedicel, of equal length, acute. Flowers 2–14, usually 5–7, horizontal at maturity, zygomorphic. Perianth segments 22–26 x 7–10(–11) mm, finely and irregularly pink-spotted rather than tessellated, usually yellow-spotted at base, ovate-lanceolate, acute; the inner somewhat wider. Nectaries placed ca. 0.5 mm above the base of the perianth segments, about 3–4 mm long at orifice, calcarate, the upper larger than the rest, the two lobes surrounding the nectary orifice very narrow, distinctly fringed and ciliate. Filaments 6–8 mm long, slender, papillose below; anthers 2–3 mm, purple, ellipsoid; pollen sculpture rugulate. Style 5–7 mm long, slender, entire, glabrous, pale green. Ovary 4–5.5 mm long, 6-angled. Capsule 14–17 mm long, subglobose, winged, toothed at the top. Seeds unknown. Chromosome number: $2n = 24$.

Flowering time: Early March–April.

Ecology and distribution: Sand dunes, shifting sands among halophytes and xerophytes, and dry slopes, c. 1000 m. Also known from Turkomania and Afghanistan.

Rhinopetalum arianum is known only from one collection in Iran: Khorasan, Torbat-e Jam, near Hari Rud, where it grows in sandy steppes. It is very close to *R. gibbosum* and *R. karelinii* Fisch. ex D. Don in aspects of nectary features, papillose filaments and styles, and also in having zygomorphic flowers, but it differs from both by having untessellated perianth segments, and shorter filaments and styles. Moreover, the basal leaves are somewhat narrower than in *R. gibbosum*. The stem in *R. arianum* is glabrous, or papillose only below the lowest leaves, while that of *R. karelinii* and *R. gibbosum* is papillose throughout.



Fig. 5. *Rhinopetalum arianum*.

Specimens examined:

Iran: *Khorasan*: Torbat-e Jam, Salehabad, near Hari Rud, associated with halophytes and xerophytes, c. 1000 m, 21.4.94, Bakhshi Khaniki 42 (GB).
 Afghanistan: *Maymana*: half way between Andkhui and Maymana, slopes rich in annual vegetation at margin of semidesert, 25.5.1962, Wendelbo 3579 (BG, K). Turkomania: *Ashkhabad*: Between Annaju and Gjaurs, south of Kara-Kumov, Nikitin (JE, W); Ashkhabad, 16.3.1898, Litwinow 2081 (W).

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NOTES ON *FRITILLARIA STRAUSSII* (LILIACEAE) IN IRAN

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ABSTRACT

A key, description, nomenclatural synonymy, citation of specimens examined, and morphological, taxonomic, ecological and karyological details are given for *Fritillaria straussii* (Liliaceae), a member of the *Fritillaria crassifolia* group, in Iran. This species differs from the other species in the group by its peculiar phyllotaxy, most leaves being opposite, the lower and upper ones sometimes in whorls of three. In most specimens seen, the lowest leaves are lanceolate but the type collection and some other collections have broadly ovate leaves at the base of the stem. It is also peculiar in that the flowers are green when young, often turning dark reddish purple when mature. The nectaries are 9–10 x 1.2–1.6 mm, green and very slightly raised in the upper part but distinctly depressed at the base. The flowering season is May to June. The species grows mainly in loose gravelly and rocky slopes, among tragacanth, shrubs or deciduous trees. The somatic chromosome number is $2n = 24$.

INTRODUCTION

Rechinger (1990) disposed of all Iranian species of *Fritillaria* in four subgenera: *Fritillaria*, *Theresia*, *Petilium* and *Rhinopetalum*, of which the latter is now accepted as distinct genus under the same name, *Rhinopetalum* (Losina-Losinskaya, 1935; Bakhshi Khaniki and Persson, 1997).

Of the four main species groups within *Fritillaria* subgenus *Fritillaria* in Western Asia and Europe, three (*Kotschyana*, *Crassidolia*, *Caucasica*) occur in Iran. No member of the *F. meleagris* group has yet been recorded from Iran, but a representative of the group (*F. latifolia*) is found in neighbouring areas of Turkey and Caucasus, and is likely to be found in northern Azarbaijan in Iran (Rix, 1977).

The aim of the present investigation has been to produce a morphologic and taxonomic revision of *F. straussii*, a member of *F. crassifolia* group, in Iran, using as much data as possible with the aid of light microscopy (LM) and scanning electron microscopy (SEM) and chromosome studies.

TAXONOMY AND DESCRIPTION

F. straussii Bornm. (Figs. 1–6).
Bornmüller, Mitt. Thür. Bot.
Ver. 20: 45 (1904).

Type: Iran, “Persia Kurdica,
Kermanschahan
(Kirmandschah) in montosi
Kuh-Sefid”, 2.5.1903. Strauss
(holo. JE, n.v.). Ic.: Furse &
Nowell, The Lily Year Book 27,
Fig. 43 (1964). —Wendelbo,
Tulips & Irises of Iran, Fig. 29
(1977). —Rix & Phillips, The
Bulb Book, p. 82, Fig. b (1981).

Bulb globose, up to 2.5 cm
in diameter, of 2 fleshy scales;
without bulbils or stolons.
Stem 12–22(–30) cm, smooth.
Leaves 5–10, green; the lowest
6–11 x 1.5–4 cm, broadly
lanceolate to ovate, often oppo-
site; the middle 2 usually oppo-
site; the uppermost 2–3, oppo-
site or whorled, linear, acute.
Flowers 1–2, broadly campanu-
late; perianth segments green
when young, often dark red-
dish-purple when mature, usu-
ally tessellate, fascia unclear; the
outer 2.5–2.7 x 0.8–0.9 cm,
oblanceolate, obtuse; the inner
somewhat wider (0.8–1.1 cm),
obtuse. Nectaries 9–10 x
1.2–1.6 mm, linear, green, very
slightly raised in upper part,
distinctly depressed at the base,
placed 5 mm above the base of
the perianth segments.



Fig. 1. *Fritillaria straussii*. Habit.



Fig. 2. *Fritillaria straussii*. Flower.

Filaments 8–10 mm long, slender, papillose. Anthers 3–4.5 mm after dehiscence, pale yellow; pollen sculpture macroreticulate, exine surface rough due to very small granulae. Style 6–10 mm long, 3-fid almost from the base, yellowish-white, papillose. Ovary 6–7 mm long, stout-cylindrical. Capsule 3–4.5 x 2.5 cm, obovoid, narrowly tapering toward the base, not winged. Seeds 8.5–9 x 6 mm, ovate in outline.

Specimens examined:

Iran: *Bakhtiari*: Kuhrang, 3.5.1969, Norwegian Volunteer Service 612 (BG). — *Kermanshahan*: Kermanshah, Kerend, 17.4.1951, Scharif 5011 (BG, K, E); Kuh-e Bimar near Deh-e Hukani, south of Kerend, 1500 m, 8.5.1975, Wendelbo & Assadi 16758 A (GB, TARI), 3.5.1994, Bakhshi Khaniki 54 (GB); Kuh-e Parrow, 1700–2100 m, stony and rocky slopes, 7.5.1975, Wendelbo & Assadi 16729 (GB, W, TARI); Strauss (JE), 1700–2100 m, 2.5.1994, Bakhshi Khaniki 52 (GB); Kermanshah, Bisutun, 24.4.1903, Strauss (JE); Kermanshah, Kuh-e Sefid, 12.5.1904, Strauss (JE, type locality); Zagros mountain, August 1918, Canbeller (K); Islamabad to Ilam, Ghallajeh pass, 1600 m, 2.5.1994, Bakhshi Khaniki 51 (GB). — *Kordestan*: Marivan, in slopes with herbs and, higher up, tragacanth vegetation replacing destroyed forest, 2000–2100 m, 7.5.1963, Jacobs 6533 (BG, K, W).



Fig. 3. *Fritillaria straussii*. Fruit.

NECTARY MORPHOLOGY

The *Fritillaria crassifolia* group is distinguished by having usually broadly campanulate flowers (narrowly campanulate in *F. poluninii*), generally nodding at maturity, and linear nectaries, half or more than half as long as the perianth segments and placed at 3–5 mm above their base. The nectaries are usually black-purplish at the base, continuing and tapering toward the tepal apex by a narrow zone divided longitudinally by a channel. The basal part of the nectaries is apparently



Fig. 4. *Fritillaria straussii*. Nectaries.

more active in nectar sugar secretion because that is usually filled with a watery fluid which seems to trickle along the median furrow, i.e. downwards in the hanging flowers.

In *F. straussii*, known from N. W. Iran and S. E. Turkey, the flowers are green when young, often dark reddish purple when mature and usually tessellated. The outer tepals are 25–27 x 8–9 mm, oblanceolate and obtuse (Figs. 2, 4). The nectaries are 9–10 x 1.2–1.6 mm, green and very slightly raised in the upper part but distinctly depressed at the base (Fig. 4). Similarly to some other members of the *F. crassifolia* group, they are surrounded by groups of round or oblong warts, not only on the margins, but also dispersed especially on the distal part of the tepal surface (Fig. 4, 5).

ECOLOGY

Flowering time: May–June.

Ecology and distribution: Loose gravelly and rocky slopes, among traganths, shrubs or deciduous trees, 1500–2100 m. Also known from S.E. Turkey.

Fritillaria straussii differs from the other species in the *F. crassifolia* group in its peculiar phyllotaxy, most leaves being opposite, the lower and upper ones sometimes in whorls of three. In most specimens seen, the lowest leaves are lanceolate, but the type collection and some other collections have broadly ovate leaves at the base of the stem [Scharif 5011 (K, E),

Wendelbo & Assadi 16758 A (GB, TARI)]. It is also peculiar in that the flowers are green when young, often turning dark reddish purple when mature. The style divided almost from the base is a further characteristic of *F. straussii*, a condition which has never been observed in other species of the *F. crassifolia* group.

KARYOLOGY

The karyotype consists of two large metacentric, four subtelocentric and six telocentric chromosome pairs (Fig. 6). The karyotype formula is $2n = 2x = 24 = 4m + 8st + 12t$. Giemsa C-banding pattern is characterized by the following major bands: centromeric bands exist in the short arms of chromosome pairs nos. 2–5, 8–9, 11–12, and in the long arms of pairs nos. 3–12; intercalary bands are absent in the short arms, but present in the long arms of pairs nos. 1 and 10; telomeric bands are present in the short arms of pairs nos. 1–2, 6–7, 9 and 12, but they are absent in the long arms; no secondary constrictions were observed; the short arm of pair no. 12 was entirely heterochromatic. Apart from these features, there are many minor bands which are mostly at intercalary positions. It is very clear from the mitotic plates and idiograms that most bands are situated at one or both sides of the centromere and that the intercalary bands are scarce. This is indeed the most characteristic feature of the C-banded karyotype in *F. straussii*.

Heteromorphy with respect to band width is comparatively less apparent in this species and was only observed in the pairs nos. 1 and 6. The karyotype was identical for all populations examined. The nuclear interphase structure is characterized by several chromocenters of different size (Fig. 6).

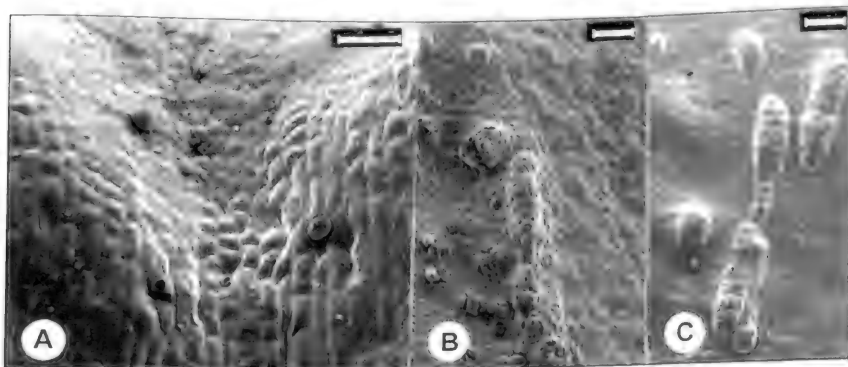


Fig. 5. *Fritillaria straussii* (A–C) SCANNING ELECTRON MICROGRAPHS OF NECTARY. A. Nectary base on outer tepal. B. Groups of warts and short ridge-like processes on nectary margin (nectary to the right). C. Warts and ridges on tepal surface. Scales: A, 100 μ m; B–C, 200 μ m.

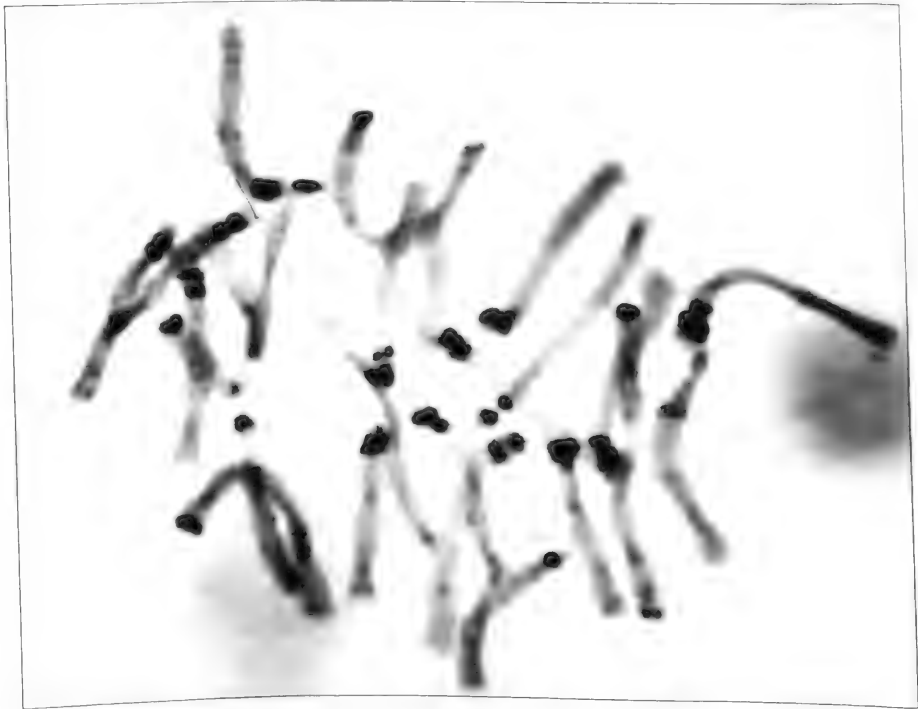


Fig. 6. *Fritillaria straussii*. Somatic chromosome number. $2n = 2x = 24$.

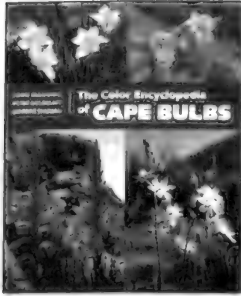
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BOOK REVIEWS

**The Color Encyclopedia of Cape Bulbs.**

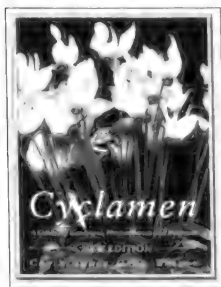
John Manning, Peter Goldblatt and Dee Snijman.
 Timber Press, Portland, OR. Hardcover, 486 pp.,
 611 color photos, 2 color maps, 2 tables, 8½" x 11",
 hardcover. \$59.95. ISBN 0-88192-547-0. 2002.

The Cape Province of South Africa is justifiably celebrated in botany for the diversity of its mostly endemic flora, and the speciose radiation of particular angiosperm families within its relatively small geographic confines. Approximately sixteen percent of this diversity is represented by geophytic plants, notably members of Iridaceae, Amaryllidaceae, and Hyacinthaceae. The greatest concentration of these plants is in the southwestern Cape, where rainfall is restricted to the winter months, and summer brings unremitting drought, but the summer rainfall eastern Cape is also blessed with hundreds of bulbs species. The bulb flora of the Cape region of South Africa continues to thrill, astound and intrigue enthusiasts of geophytic plants, and new books about this paragon of plant diversity are always welcomed. When three of the world's foremost scientific experts on these plants take pen in hand, it is an event to be celebrated.

The volume opens with a discussion of the reasons for the richness of the Cape bulb flora, the history of plant exploration in the region, and the geographic system that is used throughout the book to denote specific areas defined by keynote species. This is followed by a chapter devoted to general considerations about cultivating Cape bulbs. The third introductory chapter provides descriptions of the plant families that contribute to the Cape bulb flora, and includes keys to the genera native to the area. The main body of the encyclopedia is a treatment of the genera and species found in the region, in alphabetical order. Each synopsis begins with a generic description and cultivation notes, followed by an enumeration of the individual species. Each species is amply described, including flowering times and habitat characteristics. This section is a treasure trove of beautiful color photographs, most by Manning or Goldblatt.

The book ends with an identification key to all of the species included in the encyclopedia, a source list for seed and plants, a glossary of botanical terms, indices of synonyms and common names, and a reference list. The bibliography is heavily weighted towards the taxonomic literature cited

within the main body of the text; certain largely horticulturally oriented books about Cape bulbs are not listed. This is, however, a trivial absence. Cape bulbs have never before been so authoritatively treated between the covers of a book, or as amply illustrated. It is an essential addition to the bulb enthusiast's library.



Cyclamen, A Guide for Gardeners, Horticulturists and Botanists. Christopher Grey-Wilson. Timber Press, Portland, OR. 224 pp, 197 color photos, 40 line drawings, 12 maps, 7½" x 9½", hardcover. \$39.95. ISBN 0-88192-587-X. 2003.

Cyclamen never seems to go out of fashion. The numerous potted cultivars of the florist's cyclamen (*C. persicum*) are mainstays of the retail flower and plant shop, while the hardier species are much sought gems for the woodland and alpine garden, providing floral color in spring, summer as well as autumn and winter, and distinctive foliar accent before, after, or alongside the flowers. No one is better suited to treat the genus to a thorough horticultural monograph as Dr. Christopher Grey-Wilson, the UK's reigning Renaissance man of plants. Botanist, horticulturist, artist and writer, Grey-Wilson has produced a revised edition of his original treatise on the genus (first published in 1997).

The author begins with a personal paean to the "magic of cyclamen" that ranks with the best of garden writing. This short chapter merely whets the appetite for the riches to come. This is followed with a detailed discussion of cyclamen cultivation, propagation and pest and diseases. Chapter Four provides a complete morphological description of the cyclamen plant that includes a handy enumeration of the species grouped by flowering season. Next, the author summarizes the nomenclature, phylogeny, cytology, ecology, distribution and classification of the genus. Chapter Six is a detailed account of the known species, complete with detail drawing, numerous color photographs and distribution maps. Many horticultural monographs would be content to stop there. Grey-Wilson next provides a treatment of the many cyclamen cultivars, even indicating Royal Horticultural Society awards. Another chapter is devoted to *C. persicum* alone, detailing its history and "evolution" into the valued floral crop that it has become. This is followed by a review of cyclamen hybrids, and a (mercifully) brief account of mutant aberrations that have at times caught the fancy of cyclamaniacs. The

book finishes with an alphabetical list of all scientific names in *Cyclamen*, a discussion of conservation concerns as they relate to the genus, a subgeneric taxonomy, a species identification key oriented towards the layperson, a source list (regrettably only British nurseries are listed), a glossary, and an ample bibliography.

Cyclamen is profusely illustrated, though a number of the photos have a blue cast to them that should have been filtered during the separation process. The simple line drawings, while elegant, do not add very much to the species accounts.

Grey-Wilson clearly set out in this revised edition to provide the reader with everything he or she always wanted to know about cyclamen. The result is a peerless, exhaustively researched gem of a book that will be the authoritative reference on the genus for years to come.

—Alan W. Meerow
Miami, Florida

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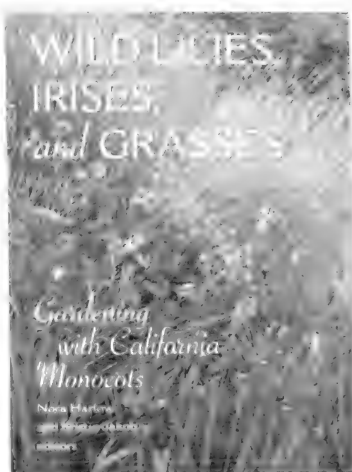
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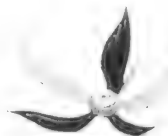
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Eucrosia aurantiaca (Baker) Pax. Die Nat. Pflanzenfam. (A. Engler and K. Prantl, eds.), 15a: 415 (1930).

Callipsyche aurantiaca Baker. Refug. Bot. 3:t. 167 (1869). Neotype: Ecuador, El Oro, Ayabamba, 200 m, Andre 4262 (K).

Eucrosia morleyana Rose. Addisonia 7: 3–4, pl. 226 (1922). Type: Ecuador, Chimborazo, Huigra, 4000 ft, Rose & Rose 22593 (holotype, US; isotypes, GH, NY, S).

Eucrosia eucrosioides var. *rauhiana* (Traub) Traub. Pl. Life 22: 62 (1966).
Callipsyche eucrosioides var. *rauhiana* Traub. Pl. Life 13: 61 (1957). Type:
 Ecuador, Azuay, Pasaje, 300 m, Rauh & Hirsch F15 (holotype, MO)

Bulb large, 7.7–10 cm long, 6–7.7 cm in diam.; tunics tan-brown; neck (2.5)5–8 cm long, 2–2.6 cm thick. Leaves 2, hysteranthous; petiole 27–35 cm long, 7.5–10 mm thick, deeply channelled for most of its length; lamina ovate-elliptic, 29–40 (50) cm long, (12) 16–22 (29) cm wide, acute or short-acuminate, basally attenuate to the petiole, thick, coarsely undulate, hypostomatic, abaxial cuticle thickly striate and non-glaucous. Scape (5) 7–9(10) dm tall, ca. 10 mm in diam. proximally, ca. 4–6 mm in diam. distally; bracts 3(5) cm long, lanceolate. Flowers (7) 10–12, (13), zygomorphic, all reaching anthesis concurrently, more or less perpendicular to the axis of the scape; pedicels (11) 22–33 mm long, 1–2 mm in diam.; perianth (2.8) 3–4 (4.4) cm long, green in bud, yellow at anthesis, rarely orange or pink, compressed laterally giving the perianth a somewhat flattened appearance; tube sub-cylindrical, 5–7 mm long, ca. 5–6 mm wide, constricted at the ovary to ca. 3.8 mm wide, concolorous with the tepals for most of its length, green only at the base; tepals spreading dorsally and ventrally to 23–29 mm wide, recurved and sometimes stained green apically; outer tepals (20) 23–29 (36) mm long, 5–6 mm wide, apiculate, lanceolate, keeled, 2 of them situated laterally, one dorsally; inner tepals 20–26 (34) mm long, obtuse, oblanceolate-spatulate, margins undulate at the middle, 2 of them ca. 9.5 mm wide and situated laterally above the 2 lateral outer tepals, the third one 5–7 mm wide, ventrally declinate and with the lower lateral tepals forming a pseudo-labellum. Stamens subequal, 8.5–11 cm long, filiform, long-declinate, ascendent in their distal 1/4, green; filaments dilated and connate in their proximal 2–3 mm; globose nectar glands present at the perianth throat, each 1–2 mm in diam.; anthers 5.5–6 mm long, oblong; pollen green, the exine mostly tectate-perforate. Style 10–11 cm long, green; stigma less than 1 mm wide. Ovary ellipsoid, 6.5–9 mm long, 4–4.5 mm wide; ovules 20 or more per locule. Capsule 2.5–3 cm long, 17–22 mm in diam.; pedicel 5–6 cm long; seeds numerous, blackish-brown, ca. 6.5 mm long, 1.5 cm wide. $2n = 46$. Flowering July–September and December–January.

ECUADOR. El Oro: between Santa Rosa and La Chorita, 0–100 m, Hitchcock 21139 (GH, NY, US). Chimborazo: Río Chanchan canyon between Naranjapata and Olimpo, terrestrial in rock wall crevices, 800

m, (ex hort), Horich ISI # 214 (UC). Between Huigra and Naranjapata, 600–1200 m, Hitchcock 20638 (GH, NY, US). Cañar: valley of Río Cañar near Rosario, 960 m, Prieto CP-18 (NY, S). Azuay: Road from Jiron to Pasaje, near Uzhcurrumi, dry, steep, rocky hillside, 840 m, Plowman et al. 4600 (GH), Plowman 7634 (F), Plowman 12024 (F). Km 97 on road from Cuenca to Saraguro, dry thorn scrub, ca. 1100 m [incorrectly typed on specimen label as 2400 m], Madison et al. 7517 (SEL). —Inhabiting semi-desert and dry, rocky canyons and hills of the lower inter-Andean valleys (100) 300–900 (1100) m. Endemic.

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